# Effects of early-life social experiences on learning and conservation in a threatened songbird

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**Thesis title:** Effects of early-life social experiences on learning and conservation in a threatened songbird

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**Thesis summary:**

Learning new behaviour is a fundamental way for animals to adjust to changes in their surroundings and is especially important for naïve juveniles. Paying attention to socially-provided information may be a way for juveniles to learn rapidly and avoid starvation or predation, so the social environment could be key in helping young animals survive. Little is known, however, about how different social experiences affect learning during early life. My PhD thesis addresses this gap in juvenile hihi (*Notiomystis cincta*), a threatened New Zealand passerine. To begin, I tested if juvenile hihi learned to forage using cues differently than adult birds and found that juveniles were less efficient learners and had to compensate by foraging for longer. This suggested they may benefit from using socially-provided information to inform behaviour. Next, I characterised the social behaviour of juveniles using a novel combination of re-sighting analysis and social network analysis on three field seasons' worth of observation data. The results demonstrated that young hihi form "gang"-like groups with little interaction with adults; these groups could function as information centres and allow knowledge to be shared amongst many naïve peers. I next conducted an experiment to test if juvenile hihi retain behaviour learned with their parents, or copy their peers when in these juvenile groups. I found that juveniles may pay attention to their parents to begin, but once independent they copy their peers and by doing so can conform to the collective behaviour of groups. Finally, I evaluated whether knowledge of social groups can help conservation management of hihi during reintroductions. We often move groups of juveniles to establish new populations but do not know if maintaining social groups could improve chances of establishment. I used social network analysis to explore whether juveniles maintained group associations once reintroduced. Juveniles moved to a new site formed new social bonds; importantly, individuals that lost more associates were less likely to survive the first few months post-release. This may be because of combined disruption of both social and physical environments during translocation. Together, my findings demonstrate how social experiences in groups have implications for learning and can help young animals overcome the challenges of being naïve during early life, particularly if environments change abruptly following human intervention.

# DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution. The thesis does not exceed the prescribed word limit of 60 000 words.

September 2018

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*In memory of Jason Campbell,*
*Tiritiri Matangi Island DOC Ranger from 2012 – 2015*

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# CHAPTER 1

# General introduction

Using information to change behaviour is ubiquitous across the animal kingdom. Through interacting with their surroundings, animals acquire information about the current environment which reduces uncertainty about how to respond appropriately (Dall *et al.*, 2005). As a result, they locate new food, avoid predators, or find mates by adjusting their behaviour to different environments across their lifetime (Wong and Candolin, 2014). Understanding the importance of information to shape behaviour has become a main focus of research for behavioural ecologists (Dall *et al.*, 2005; Schmidt, Dall and van Gils, 2010), but how animals use different types of information to maximise their fitness still remains a subject of discussion (Dall *et al.*, 2005).

Information use plays a crucial role in foraging. Animals face a constant challenge to find enough food and balance the energy requirements of living (Krebs, Kacelnik and Taylor, 1978), so accessing new resources or honing pre-existing behaviours may mean the difference between survival and starvation. Failed foraging attempts can be used to acquire information that shapes the appropriate behavioural response through progressive trial-and-error. For example, rufous hummingbirds (*Selasphorus rufus*) learn to accurately locate rewarding food patches by remembering non-rewarding attempts from initial searching (Sutherland and Gass, 1995; Hurly, 1996). In nature, however, animals often do not forage

alone, which alters how they behave. This is because encountering other individuals (both con- and heterospecifics) can lead to competition for finite food resources (Rubenstein, 1978; Krebs and Inman, 1992), but there are also advantages because peers provide information about the environment which an animal can use to change its own behaviour ("social information") (Danchin *et al.*, 2004; Dall *et al.*, 2005). Naïve animals may discover foraging locations from peers ("local enhancement" (Heyes, 1994)) (Krebs and Inman, 1992), but can also copy the behaviour of other animals directly (Lefebvre *et al.*, 1997).

The theory of how animals use social and personal information to forage effectively has been discussed extensively (Kendal *et al.*, 2005; Kendal, Coolen and Laland, 2009). Personal information is accurate but time-consuming to acquire (Templeton and Giraldeau, 1996; Giraldeau, 1997) while social information is the opposite: naïve individuals can bypass trial-and-error by using information acquired by another, but peers are not always reliable so social information may be less accurate (Dall *et al.*, 2005). Copying misinformed peers can have long-term consequences for groups, as maladaptive behaviours persist even when the initiators are no longer present (Curio et al., 1978; Laland & Williams, 1998; Pruitt et al., 2016; but see Aplin, Sheldon, & McElreath, 2017). Further, individuals can actively provide inaccurate information to deceive (Wheeler, 2009; Flower, 2011). In general, social information is thought to be most beneficial when individuals are uncertain or have poor knowledge (Galef and Laland, 2005; King and Cowlishaw, 2007) or when environments are risky, such as when there is increased chance of predation (Laland, 2004). Implicitly, understanding why animals use social information also helps to show why they are not acquiring it personally instead (Rieucau and Giraldeau, 2011). To support theory, in the past 30 years there has been an explosion of empirical examples showing that use of social or personal information (or integrating the two, see Thorogood & Davies (2016); Rieucau & Giraldeau (2011)) depends on who is learning, when and where (Templeton and Giraldeau, 1996; Galef and Giraldeau, 2001; van Leeuwen *et al.*, 2013). For example, European starlings (*Sturnus vulgaris*) only relied on social information to inform foraging choices when there was a low chance of successfully locating food by themselves (Templeton and Giraldeau, 1996). Similarly, nine-spine stickleback (*Pungitius pungitius*) used social information when their own knowledge was outdated or when food sources changed unreliably (van Bergen, Coolen and Laland, 2004). Nevertheless, there is increasing evidence that social information still plays an important role in shaping foraging behaviour in wild animals and has been shown to underpin the development of cultural traditions such as hunting mechanisms or preference for certain food types (Allen *et al.*, 2013; van de Waal, Borgeaud and Whiten, 2013; Aplin *et al.*, 2015b).

Even with the body of literature that has emerged on information use, there are remaining gaps in our knowledge. For example, we still do not understand the ontogeny of social information use, to show how early life affects what information animals pay attention to. Often while trying to understand the reasons why wild animals use personal or social information, we have limited knowledge of their life leading up to the present; however, there is recent evidence demonstrating that experiences in early life affect how animals use information later (Boogert, Zimmer and Spencer, 2013; Farine, Spencer and Boogert, 2015;

Mesoudi, 2015). Therefore, without an understanding of how early-life experiences affect information use in young, naïve animals, we cannot fully explain why animals behave as they do. This also reflects the general paucity of research about early life behaviour, which is particularly apparent in certain taxa such as birds (Cox *et al.*, 2014).

In this thesis, I focus on how juvenile birds use information to inform foraging behaviour in their first few months of independent life. I explore how young birds learn about a novel food in comparison to adults, to demonstrate the challenges that juveniles face when learning to forage. I then describe the structure of juvenile social groups and quantify their social interactions to start to understand how groups provide opportunities for juveniles to inform foraging behaviour. I go on to test how juveniles make foraging decisions when provided with social information at different points of their early life, to understand what early-life experiences might be important to inform their behaviour. Finally, I test if knowledge of social groups can be applied to inform a species' conservation management.

## *Does age affect foraging and learning?*

Learning may be particularly challenging for young animals. Experience plays a crucial role in honing behaviour (Barnard, 2004) but juveniles have had little opportunity to gather such experience (Galef and Laland, 2005). Therefore, juveniles often show less efficient behaviours compared to adults. Birds are one taxon where a range of observational field studies clearly show that individuals in their first year of life acquire less rewarding food items than adults or take longer or more attempts to reach the same gain (Table 1.1). While efficiency improves with experience, suggesting a role for learning (Vince, 1964; van Horik *et al.*, 2018), the consequences of inefficiency can be severe. Juvenile birds often show extensive first-year mortality (particularly passerines (McKim-Louder *et al.*, 2013)) in part due to starvation (Sol *et al.*, 1998; Daunt *et al.*, 2007; Naef-Daenzer and Grüebler, 2016), although predation also plays an important role (Sullivan, 1989; Griesser *et al.*, 2017). Thus, juveniles need to acquire new behaviours, and acquire them quickly.

In Chapter 2, I test how juvenile and adult songbirds learn about a novel foraging task to complement the few previous studies that have experimentally tested the effects of age and inexperience on learning in a wild setting (Mirville, Kelley and Ridley, 2016; Shaw, 2017). This experiment provides a base for a central theory for the rest of my thesis: that juveniles may benefit from using social information to improve their foraging decisions.

**Table 1.1.** Summary of studies demonstrating age differences in avian foraging behaviour. Abbreviations: ind. = individuals; obs. = observations; y = year. Findings show that young birds (under one year) forage less effectively than adults, but foraging improves with time.

| Species | Comparison | Outcome | Citation |
|---|---|---|---|
| **Blackbird**<br>*Turdus merula*<br>*N* = 284 ind. | 1 – 2y vs. adults | 1y 50% less successful than 2y.<br>All young foraged less successfully than adults. | Desrochers (1992) |
| **American robin**<br>*Turdus migratorius*<br>*N* = 41 ind. | Juveniles (c. 5 months) vs. adults | Juveniles took 136% longer and 161% more steps to capture food.<br>Juveniles acquired 25% less food per unit time. | Gochfeld and Burger (1984) |
| **Oystercatcher**<br>*Haemoptus ostralegus*<br>N = 844 obs. | 1st-y vs. adults before/after winter (6 months) | Juvenile foraged 66% less efficiently and ate smaller prey before winter.<br>No age difference after winter. | Goss-Custard and Durell (1987) |
| **Magpie jay**<br>*Calocitta formosa*<br>*N* = 11 ind. | Fledge – 14-month juveniles vs. adults | Fewer juveniles harvested prey.<br>Independent juveniles spent longer foraging.<br>No age difference in harvest rates after 160 days. | Langen (1996) |
| **Mockingbird**<br>*Mimus polyglottos*<br>*N* = 337 obs. | 1 – 2-month juveniles vs. adults | Juveniles had lower captures/attempt and captures/min.<br>Juveniles captured fewer large arthropods. | Lee *et al*. (1987) |
| **Blue heron**<br>*Ardea herodias*<br>*N* = 817 min. obs. | Newly-fledged juveniles vs. adults | Pace and strike rates similar between ages, but juveniles captured fewer prey successfully. | Quinney and Smith (1980) |
| **Little blue heron**<br>*Florida caerulea*<br>*N* = 89 ind. | Fledge – 18-month juveniles vs. adults | Juveniles missed prey more often.<br>Juveniles captured lower weight of prey/min. | Recher and Recher (1969) |
| **Rock dove**<br>*Columbia livia*<br>*N* = 180 flocks | Juvenile vs. adult | Juveniles foraged less rapidly.<br>Juveniles were more vulnerable to competition. | Sol *et al.* (1998) |

## *Why do juveniles form groups?*

If learning is challenging for naïve juveniles, then they might have strategies to compensate. Using socially-provided information to learn may be an important way that juveniles can bypass their own inexperience (Galef and Laland, 2005). Information trade-off theory predicts that a lack of information or increased risks from learning alone will favour social information use (Kendal *et al.*, 2005). Empirical studies have also demonstrated that juveniles learn more efficiently and with greater chance of success when they associate with others (Noble, Byrne and Whiting, 2014). Therefore, early-life social experiences may be a crucial way that juveniles learn new foraging behaviours, but often little is known about the early-life period and so there is limited understanding of how different experiences determine behaviour.

Parents could provide learning opportunities. In some species, prolonged periods of parental care are associated with acquisition of complex foraging behaviours, suggesting that the time spent with parents is a crucial way for offspring to acquire skills (Heinsohn, 1991; Hunt, Holzhaider and Gray, 2012). Juveniles may be able to devote more time to trial-and-error learning while being provisioned by parents (Davies, 1976; Heinsohn, 1991; Tebbich *et al.*, 2001; Truskanov and Lotem, 2017), or learn socially via local enhancement (Truskanov and Lotem, 2015) and imitation of parent's actions (Truskanov and Lotem, 2017). In some cases, parental care includes teaching (potentially with the additional assistance of non-breeding helpers) (Thornton, 2006; Thornton and Raihani, 2010). However, other examples suggest juveniles may learn equally from parent and non-parents (Hatch and Lefebvre, 1997). This questions whether the presence of the parent in particular is important or if learning arises more as a product of parents and offspring being in the same place at the same time during parental care. If the latter, then other social associations could also be important for juveniles.

Continued opportunities to gather social information could be one reason why many juveniles are more social than adults during their first year of life, particularly in mammals and birds (Ward and Webster, 2016). Juveniles tend to aggregate closer and in greater numbers in early life (Catterall, Kikkawa and Gray, 1989; Delestrade, 2008), with groups becoming less cohesive as they grow older (Kruijt, 1964; Wilson, 1973; Rowell and Chism, 1986). However, the structure of social groups varies. Many flocks, schools, or herds comprise of both juveniles and adults (for example, Parid tit flocks, see Saitou (1978)), but other groups can be more juvenile-dominated (Hinde, 1952; Ward and Zahavi, 2008; Dall and Wright, 2009). Groups are also comprised of related (Marzluff and Balda, 1992) or unrelated individuals (Saitou, 1978; Hirsch *et al.*, 2013). Finally, ecological conditions modulate the extent and duration of grouping (Godfrey, Sih and Bull, 2013; Farine *et al.*, 2015). Thus, group dynamics affect both the opportunities juveniles have to learn socially (Coussi-Korbel and Fragaszy, 1995; Seppänen *et al.*, 2007) and the information they encounter during this critical social period (Laland, 2004; Kendal *et al.*, 2005).

To understand social information transmission opportunities for juveniles and how social experiences shape their behaviour, we must first quantify their social behaviour before we investigate the outcomes of such associations. Thus, in Chapter 3, I quantify the structure of juvenile groups. I use a novel combination of re-sighting analysis and social network analysis to identify patterns in grouping behaviour across space and time. I then analyse how social associations depend on age structure and space use. With an understanding of the opportunities for (and potential downsides of) social information sharing in groups, in Chapter 4 I go on to test how social experiences with parents interact with experiences in groups to determine juvenile foraging choices.

## *What are the benefits of social groups for conservation?*

Studies of behaviour are important to conservation biology when they help predict how animals will respond to particular management approaches (Sutherland, 1998). Despite some past criticisms (for example: Caro (2007)), conservation behaviour has become a growing field of interest (Greggor *et al.*, 2016). To counter criticisms, Buchholz (2007) highlighted three main contexts where behaviour was relevant to conservation. Understanding behaviour can be important to: (1) prevent biodiversity loss: for example, testing how predators respond to exclusion fencing can help develop the best design to reduce predation of predator-naïve species in protected areas (Moseby and Read, 2006); (2) mediate compromises with economic development, such as behavioural interventions that prevent human/wildlife conflict (King *et al.*, 2009); and (3) promote species or ecosystem restoration: for example, understanding how different release techniques affect dispersal (Hardman and Moro, 2006) following reintroductions to establish species in areas where they have previously become extinct (IUCN/SSC, 2013). One way that behavioural studies can address all of these contexts is by testing the response of animals to management strategies to inform later conservation practices (Greggor *et al.*, 2016).

Understanding the importance of social behaviour to species or individuals may have particular importance during reintroductions. Survival is especially challenging in the "establishment" phase following release, when animals need to overcome post-release effects of environmental novelty to find food and avoid predation (Batson, Abbott and Richardson, 2015). If social groups can help inform foraging behaviour for animals with little personal experience, then sociality may be important when animals need to adjust behaviour following abrupt human-induced changes in environment (Wong and Candolin, 2014). Maintaining group composition may therefore be important (IUCN/SSC, 2013) if the collective knowledge of familiar groups affects behaviour in new sites (Swaney *et al.*, 2001). One example where understanding the sociality of a species has benefitted its conservation (Blumstein, 2010) is the black-tailed prairie dog (*Cynomys ludovicianus*). Following over a decade of study this species was known to be highly social and form family groups (Hoogland, 1995), which suggested that sociality could be important during reintroductions (Truett *et al.*, 2001). When tested experimentally,

juveniles showed higher survival post-release if they learned socially about predators from adults (Shier and Owings, 2007), and translocating intact family groups rather than mixed ones also increased survival during establishment (Shier, 2006). Further, individual-level sociality has also been shown to be important for surviving abrupt changes in environment: wild horse (*Equus calabus*) foals with more associates were more likely to survive following the loss (removal) of nearly half of their herd (Nuñez, Adelman and Rubenstein, 2015). However, understanding the consistency of individual-level sociality is still in its infancy (Godfrey, Sih and Bull, 2013; recent studies that begin to address this topic include: Formica *et al.*, 2016; Firth *et al.*, 2017). For known social species or cohorts, combining analysis of social group changes with hypothesis-driven research can test the outcomes of managing groups during reintroductions (Taylor *et al.*, 2017). Understanding social group changes and their effects could also help our understanding of the evolutionary and ecological importance of animal sociality (Pinter-Wollman *et al.*, 2013; Snijders *et al.*, 2017).

In Chapter 5, I test whether the knowledge of sociality gathered in previous chapters can be used to inform reintroductions. I investigate changes in group structure and individual sociality following release, test whether maintaining familiar social groups affects social changes, and assess the consequences of social changes for survival at a new site.

## *Using social network analysis to study social behaviour*

Non-uniform associations in groups of animals can be represented as social networks (Krause, Lusseau and James, 2009; Krause *et al.*, 2015) which provide a way to analyse the presence and consequences of social relationships. Many studies have now demonstrated the presence of networks in animal groups (Croft, Krause and James, 2004; Croft *et al.*, 2005; Mourier, Vercelloni and Planes, 2012; Farine, 2015) and variation in how they are structured (Lusseau, 2003; Croft *et al.*, 2005; Carter *et al.*, 2013; Hirsch *et al.*, 2013; Webster *et al.*, 2013; Farine, 2014; VanderWaal, Wang, *et al.*, 2014). We have also begun to understand the implications of such structure for finding food (Aplin *et al.*, 2012; Allen *et al.*, 2013; Snijders *et al.*, 2014), disease dynamics (Drewe, 2010; VanderWaal, Atwill, *et al.*, 2014), and mate choice (Oh and Badyaev, 2010). Often, an individual's number of associates is a key determinant of both advantages and disadvantages of group living: more sociable individuals (higher "degree centrality" as they are also inherently more centralised (Krause *et al.*, 2015); (Figure 1.1)) find food faster (Aplin *et al.*, 2012) but are also more susceptible to disease (Drewe, 2010). Networks likely play a key role in the stability of groups and populations, although the direction of causality between associations and environment is still less well understood (Wey *et al.*, 2008; Sih, Hanser and McHugh, 2009; Pinter-Wollman *et al.*, 2013; Kurvers *et al.*, 2014). Finally, a recent review suggested that we can now use social network analysis in fields such as conservation behaviour to understand how disturbances might affect populations and the outcome of management actions (Snijders *et al.*, 2017).

Advances in technology have vastly increased the scope of network analysis in wild animals (Farine and Whitehead, 2015). Fitting individuals with tags (such as Passive Integrated Transponders, PIT tags) has the potential to collect a large quantity of high-quality data to infer associations between individuals in spatial or temporal proximity (for example: Aplin *et al.*, 2012; Ryder *et al.*, 2012; Levin *et al.*, 2015; Strandburg-Peshkin *et al.*, 2017). However, care is needed to relate data collected using proximity as a proxy for associations (for example, as temporally-similar visits to feeders) to real-life behaviour, particularly when networks constructed using different methods are not always comparable (Boogert *et al.*, 2014; Castles *et al.*, 2014). Therefore, validating remotely-collected data against observations of animals may be a powerful way to understand how network analysis relates to animal social behaviour. This has not always been conducted in the recent numerous studies relying on remotely-collected network data, although some authors have addressed this issue (Mennill *et al.*, 2012; Boyland *et al.*, 2013; Farine, 2015; Psorakis *et al.*, 2015).

I use social network analysis throughout my thesis to (1) investigate patterns in the structure of animal groups and how these relate to real-life interactions (Chapter 3); (2) understand how associations affect foraging behaviour (Chapter 4), and (3) test how networks change following a disruption during a reintroduction event and understand the consequences of social disruption for survival (Chapter 5). Throughout my chapters, I also refer to Appendix 2 where I present several tests of network reliability.

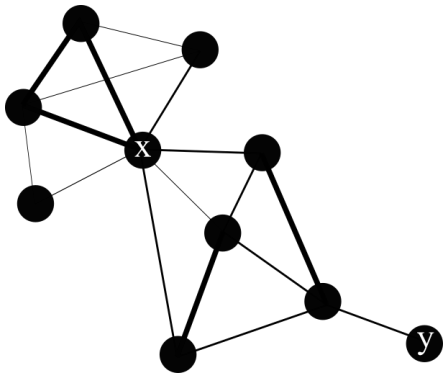


**Figure 1.1.** Representation of an animal social network. Each black circle (node) represents an individual and lines connecting circles (edges) represent an association; thicker lines indicate stronger associations (for example, individuals were repeatedly seen together in a group). Individual x has connections to seven other animals and is more centrally placed in the network and more social, while individual y only associates with one peer. Thus, individual x has higher degree centrality (Krause, Lusseau and James, 2009).

## *Hihi as a study system*

In this thesis, I address my research questions using hihi (stitchbird, *Notiomystis cincta*) as a study system. Hihi are sexually dimorphic passerines (Figure 1.2) endemic to New Zealand and the only members of family *Notiomystidae* (Driskell *et al.*, 2007). They inhabit North Island forest where they forage on a range of fruits, nectar and invertebrates (Craig, 1985; Rasch and Craig, 1988; Roper, 2012). Proportions consumed of these three food types vary among seasons and between sexes, although variation by age has not been formally quantified (Rasch and Craig, 1988; Roper, 2012; Walker *et al.*, 2014). Hihi became extinct on mainland New Zealand in the 1880s and were reduced to a single population on Hauturu-o-Toi (Little Barrier Island; Figure 1.3), likely due to the introduction of non-native mammalian predators such as rats (*Rattus rattus* and *R. norvegicus*) (Angher, 1984). As a result, the species is now classified as “Vulnerable” on the IUCN Red List (Birdlife International, 2017). Hihi have since been reintroduced back to parts of their range, including Tiritiri Matangi Island in 1995 (a 2.5km scientific reserve located off the coast of Auckland; 36°36'00.7"S, 174°53'21.7"E; Figure 1.3) (Armstrong and Ewen, 2001).

Tiritiri Matangi was largely deforested through human activity until 1984 but has been replanted with native flora (some old growth forest remained in gully areas). Its hihi population has become a focal study site for research over the past 23 years (Thorogood *et al.*, 2013). Hihi on Tiritiri Matangi nest in provided boxes (on average one non-ringed juvenile located and ringed post-fledging each year of the three field seasons of this PhD, which indicates a very limited number of natural nesting attempts occur). This has made it possible for the population to be monitored every year since its reintroduction to record breeding attempts, colour-ring chicks in the nest so each individual can be identified by sight, and collect blood samples to maintain a genetic pedigree. Hihi are provided with ad-libitum supplementary food (sugar water), which is available year-round at feeding stations. Such level of detail on the lives of individual wild birds is rare. Combined with the solid foundation of knowledge from years of previous research, hihi provide an ideal study system to investigate how early-life social experiences affect foraging behaviour, with an opportunity to test if sociality can be implemented in conservation management.


**Figure 1.2.** Hihi on Tiritiri Matangi Island: (a) adult male hihi; (b) adult female hihi; (c) juvenile hihi, which resemble adult females immediately after fledging but lack the speckled underbelly. Juvenile males begin to moult into adult plumage from approximately three months of age. Photo credits: Malcolm and Annette de Raat.

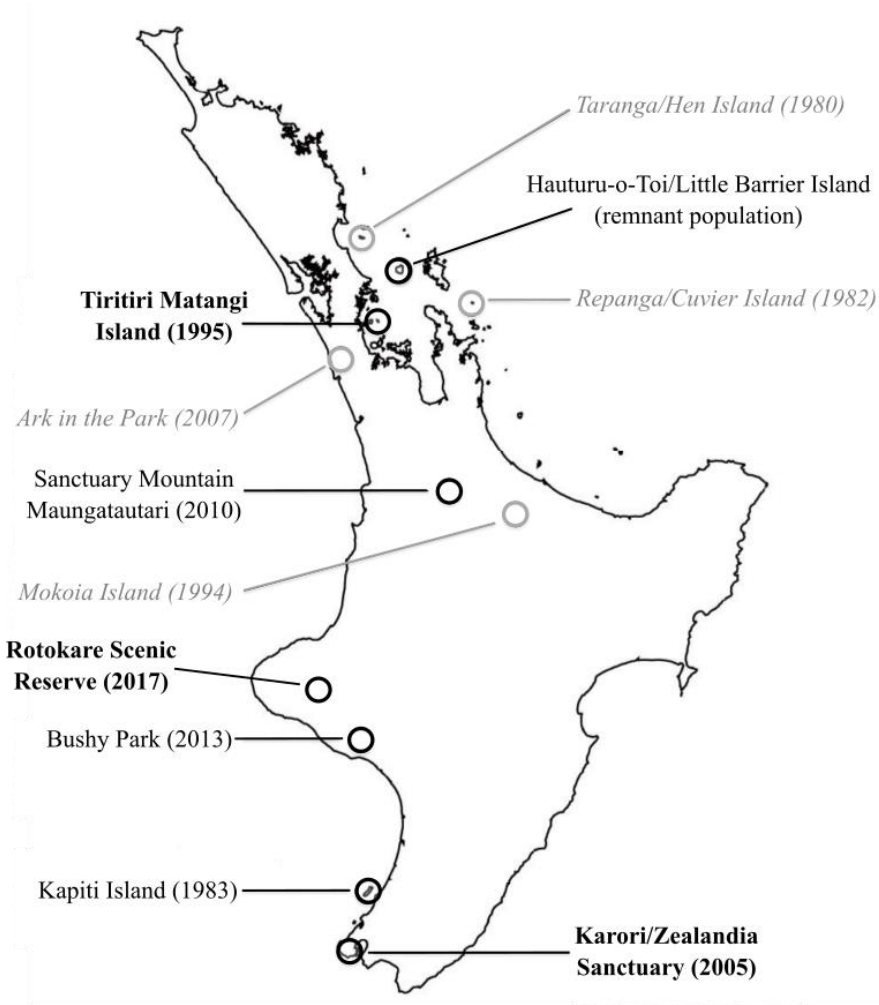


**Figure 1.3.** Location of all extant hihi populations (black circles), and failed reintroduction sites (grey circles; italic font) in the North Island of New Zealand. All dates represent initial time of reintroduction. The main study site for this thesis is highlighted in bold (Tiritiri Matangi Island), plus two additional sites also referred to throughout the Chapters (Zealandia Sanctuary/Rotokare Scenic Reserve). Adapted from Thorogood et al. (2013).

Juvenile hihi (Figure 1.2) spend approximately 28 days in the nest prior to fledging and are then cared for by parents for two weeks before dispersing. However, only approximately 50% of juveniles reach their first breeding season to be successfully recruited into the population (Low and Pärt, 2009). Predation is unlikely to be a major contributor to this mortality. Hihi have two natural extant predators, the kārearea (NZ falcon, *Falco novaeseelandiae*), and ruru (morepork, *Ninox novaeseelandiae*). While kārearea prey on a range of bird species including hihi (Panfylova *et al.*, 2016), they are absent on Tiritiri Matangi, and the diet of ruru mainly consists of invertebrates so likely account for few juvenile deaths (Busbridge, 2017). On the other hand, evidence from studies contrasting survival under different availability of supplementary food supply suggests that food limitation may be key to the viability of several hihi populations (Armstrong and Ewen, 2001; Chauvenet *et al.*, 2012). Therefore, starvation may be particularly pertinent to juvenile survival (Rasch, 1985). According to anecdotal reports collected during post-breeding surveys each year, juvenile hihi congregate in gully sites across the island; however, no data existed on the first few post-fledge months for hihi prior to the start of this PhD, and we did not know if the time spent with parents or peers provided opportunities for social learning. The ideal setting of hihi on Tiritiri Matangi means I had the opportunity to determine hihi social behaviour in Chapter 3 and test the links between juvenile sociality and foraging at the individual level in Chapter 4.

Reintroductions have been a major component of hihi conservation since the 1980s to re-establish populations in the species' previous range (Thorogood *et al.*, 2013). However, determining successful reintroductions has been challenging, and throughout the years reintroductions have had mixed success (Figure 1.3). We are beginning to understand how conservation management approaches (such as delaying release) negatively impact survival chances (Richardson *et al.*, 2013), but overall there is still much scope for improvement in reintroduction practices as initial mortality post-release can be high (Armstrong *et al.*, 2017). Additionally, established reintroduced populations are all currently supported by intensive management (including supplementary feeding). Thus, understanding the components that lead to viable populations remains a central focus of hihi research. The population on Tiritiri Matangi now serves as the source population for translocations so this creates an opportunity to related detailed behavioural studies directly to current conservation (Armstrong and Ewen, 2013; Thorogood *et al.*, 2013). Further, reintroductions since 2005 have involved moving a proportion of the juvenile cohort (Thorogood *et al.*, 2013). Therefore, exploring the importance of social groups for juveniles and testing how our management of social groups affects survival post-release may help inform future conservation management for this threatened species.

## *Thesis format*

Each chapter of this thesis (excluding general introduction and discussion) has been prepared in manuscript format for publication. As such, some information is repeated in each chapter and chapters are written from a plural perspective (“we”, “our”). Where possible, I refer to other chapters to minimise repetition. Appendix 1 contains all Supplementary Material referred to throughout the thesis; Appendix 2 contains validation of observation and social network methods used throughout this thesis; and Appendix 3 contains a published report for a grant I received during my PhD to fund a minor extra study on juvenile hihi behaviour.

# CHAPTER

# 2

# Older and wiser? Age differences in foraging and learning by a threatened passerine

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Birds use cues when foraging to help relocate food resources, but natural environments provide many potential cues and choosing which to use may depend on previous experience. Young animals have less experience of their environment compared to adults, so may be slower to learn cues or may need to sample the environment more. Whether age influences cue use and learning has, however, received little experimental testing in wild animals. Here we investigate effects of age in a wild population of hihi (*Notiomystis cincta*), a threatened New Zealand passerine. We manipulated bird feeders using a novel colour cue to indicate a food reward; once hihi learned its location, we rotated the feeder to determine whether the birds followed the colour or returned to the previous location. Both age groups made fewer errors over trials and learned the location of the food reward, but juveniles continued to sample unrewarding locations more than adults. Following a second rotation, more adults preferred to forage from the hole indicated by the colour cue than juveniles, despite this no longer being rewarding. Overall, juveniles spent longer in the feeder arena to reach the same proportion of foraging time as adults. Combined, these results suggest that juveniles and adults may use an “explore and exploit” foraging strategy differently, and this affects how efficiently they forage. Further work is needed to understand how juveniles may compensate for their inexperience in learning and foraging strategies.

## *Introduction*

It is well-established that animals can learn to associate cues with food resources (Kamil and Roitblat, 1985; Brodbeck, 1994; Hurly and Healy, 2002; Boogert, Monceau and Lefebvre, 2010), but natural environments provide many potential cues, and not all remain informative across time or space. Therefore, animals should use information from previous experiences to update foraging choices (Dall *et al.*, 2005; Herborn, Alexander and Arnold, 2011; Thornton and Lukas, 2012). Younger individuals, however, have had fewer opportunities to gain experience (Galef and Laland, 2005). Consequently, this could affect how long it takes young animals to learn foraging behaviours compared to more experienced adults, and reduce their survival when there is competition for limited food resources (Sullivan, 1989; Whitfield, Kohler and Nicolson, 2014). Impacts on juvenile survival may be especially critical in threatened species, where there are already a reduced number of juveniles contributing to population viability (Melbourne and Hastings, 2008). Despite the body of research exploring how juveniles learn (Vince, 1958; Weed, Bryant and Perry, 2008; Benson-Amram and Holekamp, 2012), there are scant examples in species of conservation concern where understanding juvenile behaviour may inform conservation strategies (Sutherland, 1998; Buchholz, 2007).

Juveniles are often less neophobic than adults, and interact with novel learning tasks more readily (Biondi, Bó and Vassallo, 2010). Juveniles can also be more persistent at learning tasks compared to adults (Vince, 1958; Benson-Amram and Holekamp, 2012; Manrique and Call, 2015). Readiness to approach a task and interact with it may allow juveniles to innovate (Reader and Laland, 2001; Morand-Ferron *et al.*, 2011). However, a tendency to approach and explore new tasks does not lead to learning, if past interactions do not inform future behaviour. Therefore, juveniles can be at a disadvantage if they do not learn appropriate responses; for example, less neophobic juvenile caracara (*Milvago chimango*) were found to be slower to solve a learning challenge (Biondi, Bó and Vassallo, 2010). Furthermore, juveniles are often less able to generalise and use appropriate learned cues across variable contexts (Weed, Bryant and Perry, 2008; but see Bonté, Kemp, & Fagot, 2014; Thornton and Lukas, 2012). This could lead to less efficient foraging; for example, if juveniles continue to sample more food sites to acquire information then they may return to non-rewarding sites more often (Wunderle and Lodge, 1988; Naef-Daenzer, 2000), rather than applying what they have already learned and forage optimally (Krebs, Kacelnik and Taylor, 1978). However, disentangling what drives differences in learning between adults and juveniles can be challenging if age classes also differ in body size or diet (Marchetti and Price, 1989). For example, juvenile meerkats (*Suricata suricatta*) were less likely to solve a puzzle box task than adults, but this was attributed to them lacking the physical capability of adults due to their size difference, rather than a learning effect between age groups (Thornton and Samson, 2012). Passerine birds provide an opportunity to test age differences without these potential confounds; as juveniles reach adult body size relatively quickly and by independence from parents (Case, 1978) age groups should not differ in their physical capabilities to solve learning tasks.

Despite being similar to adults in body size, juveniles of many bird species do not forage as effectively as adults (Ashmole and Tovar, 1968; Gochfeld and Burger, 1984; Schuppli, Isler and van Schaik, 2012). In the wild these conclusions are largely based on field observations (Marchetti and Price, 1989; Heinsohn, 1991; Desrochers, 1992), and the few direct comparisons of adults' and juveniles' learning using experimental tests have found variable results across different species and tasks. For example, juvenile Australian magpies (*Cracticus tibicen dorsalis*) were less likely to solve a learning task than adults (Mirville, Kelley and Ridley, 2016), but in North Island robins (*Petroica australis*), there were no age differences in how long it took individuals to reach a learning criterion in two different tasks (Shaw, 2017). Therefore, more data is needed to assess differences in learning between juveniles and adults in a wild setting and to understand how birds apply information when environments change.

Here, we examined age differences in learning by a wild bird species of conservation concern. We presented a novel foraging task to wild adult and juvenile hihi (stitchbird, *Notiomystis cincta*), a nectarivorous passerine bird endemic to New Zealand, to investigate if juveniles learn differently from adults. We designed a food-cue learning task by manipulating hummingbird-style nectar feeders to track individual learning patterns. Birds learned the location of feeding holes that allowed access to sugar water, and holes were marked by a visual cue. We then moved the position and/or changed the cue to investigate how hihi learn to rely on cues to find food. Studying food-cue learning in hihi has particular relevance for this threatened species (listed as "Vulnerable" by Birdlife International (2017)), as conservation efforts rely on supplementary feeding (Chauvenet *et al.*, 2012). Furthermore, seeding new populations of hihi involves translocation of juveniles to new sites (Thorogood *et al.*, 2013), so understanding how they acquire information about food may be key for optimal design of feeding protocols. Learning about food, however, has not been investigated in hihi before.

We predicted that: (i) hihi would learn to find the rewarding hole and be more likely to visit it first as trials progressed, to suggest they learned an association between a cue and reward. Thus, over time, birds would also reduce the proportion of non-rewarding holes they visited. However, based on evidence from the many previous observations of foraging behaviour in adult and juvenile birds, we predicted age-related foraging differences so that(ii) juveniles would be slower to learn and continue sampling for longer (shown by continuing to visit more holes). After cues changed, we also predicted that (iii) adults would be more likely to follow the visual cue than juveniles to relocate the reward hole more quickly.

## *Methods*

### STUDY POPULATION

We carried out this study in the population of hihi at Zealandia Ecosanctuary in Wellington, New Zealand (41°17'24.2"S, 174°45'13.2"E). Hihi were reintroduced here in 2005, with a breeding population of c.100 birds at the time of our study in May 2015. Male and female hihi are sexually dimorphic, and juveniles were moulting into adult plumage during our study. As part of the management of hihi at Zealandia, each bird is identifiable by a unique combination of coloured leg rings, with one colour indicating its hatch year. We could thus track the learning of individual hihi and distinguish juveniles (from the 2014-2015 breeding season).

### EXPERIMENTAL DESIGN

We conducted the experiment at one of the four permanent supplementary feeding sites that provide sugar water year-round. We chose this site because it was used by the majority of the population (*N* = 78 birds). Food is normally provided in a square, steel-framed cage (0.5m$^2$) that allows entrance of hihi (and similarly sized bellbirds, *Anthornis melanura*), but not larger competitors. For our experiment, we modified the cage to make entry to the feeder arena possible through one side only. This prevented confusion over spatial cues as individuals always approached the feeder bottle from the same direction (Figure 2.1). Every hihi that visited the feeder located and used this restricted entry point. Although the cage was not novel to the birds, the feeder bottle was. Sugar water is normally provided in a clear plastic covered dish with a feeding trough. Instead, we used a 400ml clear plastic bottle attached to a Perky Pet® feeder base (213 Pop Bottle Hummingbird Feeder, c.15cm base diameter and c.5cm between holes) that normally allows access to sugar water from three feeding holes. For the purposes of the experiment, we blocked two of the holes with clear tape to prevent access to the sugar water in the reservoir below. During the experiment we observed hihi attempting to feed from these holes, showing they were a suitable deception. The third hole remained open and allowed access to the sugar water ("reward hole").

We conducted our experiment in three stages where we changed either the position or marking of the rewarding hole (indicated in the text by a capital letter, Figure 2.1c):

(1) Hole A was rewarding and marked with a white circle. Holes b and c were non-rewarding and marked with black circles. We used black and white as they are achromatic and avoided any existing preferences or biases towards colours; we further checked for any effect of black and white biases in later analyses Stage 1 continued until the number of completely new individuals arriving at the feeder arena per day declined below five (to include as much of the population

as possible during the entire experiment), and the majority of birds attempted the reward hole first in each of three successive trials (learning criterion set *a priori*). This took five days.

(2) Hole B was rewarding and marked with a white circle, while holes a and c were non-rewarding and marked with black circles. Thus, in this stage the colour cue indicated the rewarding hole as it did in Stage 1, but the hole was in a different location. This meant we could test if hihi had learned to associate the visual cue with the food reward, or continued to attempt the previously rewarded location. Stage 2 ended after five days so it was consistent with Stage 1.

(3) Here we switched the colour cue but not the spatial location of the reward, so hole B was still rewarding (as in Stage 2), but it was now marked with a black circle. We marked a non-rewarding hole (hole c) with the white circle. If hihi associated the visual cue with a food reward, they should be more likely to follow the white circle and attempt the non-rewarding hole c. This was a control to exclude the possibility that hihi were simply detecting the open hole, rather than following the colour cue. We could also determine if hihi switched cue use between Stage 2 and Stage 3. This stage was run for 3 days because here we were interested in capturing the first return of previously recorded hihi, and not any further learning.

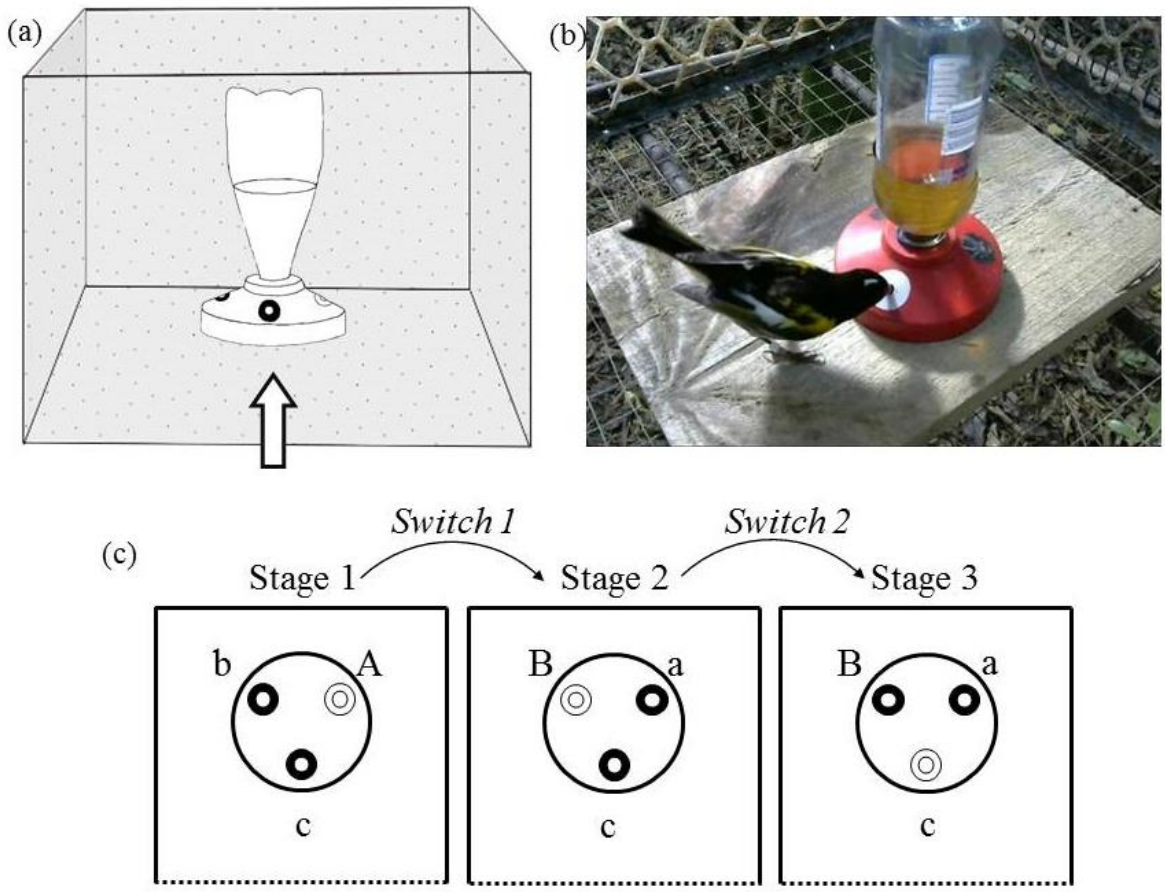



**Figure 2.1.** The novel feeder bottle learning task. (a) Diagram of the feeder arena and feeder bottle (white arrow shows the side through which hihi could enter); (b) the feeder arena in situ, with an adult male hihi feeding from the reward hole after entering from top left of picture; (c) the three stages of the experiment. Within the arena (square), the feeder bottle (large circle) shows colour markers (black, white), reward hole position (uppercase letter label), and non-rewarding holes (lowercase letter). Dashed line indicates side from which hihi could enter the arena.

During all stages, we presented the feeder bottle for 3 hours (1000-1300h) per day. We collected data using field observations (by VF, from the same position c. 8m from the feeder) and video recordings from a webcam (Logitech® C270 HD) in the upper right corner at the back of the cage. For each bird's visit to the arena ("trial"), we recorded entry time (recorded when a bird had half of its body through the mesh on the feeder entry side), individual identity, age (adult or juvenile), sex, which holes the bird attempted to feed from, and time spent feeding at the reward hole. A feeding attempt was recorded if a hihi placed its beak at a hole entrance (Figure 2.1b), or if a hihi paused next to a hole (approximately one second) and turned or cocked its head towards it. Feeding at the reward hole stopped when a bird removed its beak from a hole and moved away at least as far as its own body length. If the hihi then returned to the same hole after a cessation of feeding, this was classed as a new feeding hole attempt.

The presence of conspecifics during the experiment was recorded to account for social influences on hole choice (e.g. via local enhancement (Laland, 2004), or competition (Harper, 1982)). If no hihi was present in the feeder arena for at least 30 seconds before the focal bird, these trials were "alone" (Aplin *et al.*, 2012). "Semi-social" trials were when other hihi were present in the feeder arena less than 30 seconds before the focal bird. Finally, "social" trials were where another hihi was present in the feeder arena at the same time as the focal bird. There was no bias in distribution of social category between the two age classes (Chi-square test: $X^2_2 = 2.81$, $P = 0.25$).

**DATA ANALYSIS**

All data were analysed using R (version 3.3.1) (R Core Team, 2017).

**Learning to locate the reward**

From each trial we recorded (i) whether the reward hole was attempted first, (ii) the total number of holes attempted and (iii) the number of times an unrewarding hole was attempted. This allowed us to measure learning (if hihi became more likely to visit the rewarding hole first over trials), assess sampling behaviour (how many extra holes they visited over trials), and compare learning patterns before and after birds experienced a switch of reward location. For each bird we included the first 14 trials from Stage 1 and the first 8 trials from Stage 2 as fewer than three birds (per age group) came to the feeder arena more times than this (number of trials ranged from 1 – 44, no significant difference in number of trials made by adults and juveniles: Wilcoxon rank sum test, $W = 788$, $P = 0.78$).

Some individuals did not arrive during Stage 1 so their first opportunity to learn occurred during Stage 2 (Stage 1: $N = 59$; Stage 2: $N = 12$). Therefore, we labelled all trials within one stage as a learning sequence (LS) to account for changes in setup or environmental conditions. However, in both stages the reward hole was equidistant from the entry side, both times it was marked with a white circle, and overall there was no difference in which hole was first attempted in the first trial whether LS1 occurred during Stage 1 or 2 (Fisher's exact test: adults: $N = 34$, $P = 0.67$; juveniles: $N = 23$, $P = 0.51$).

We used Generalised Linear Mixed Effects Models (GLMM), implemented with the lme4 package (Bates *et al.*, 2015, version 1.1-7) and error distributions appropriate for the data. The probability of attempting the reward hole first (an indication of learning) was analysed as a binary response variable ("yes" = 1, "no" = 0) with a binomial error distribution. Sampling behaviour (an indication of accuracy) was analysed using a Poisson error distribution for the number of holes attempted, and a binomial error distribution to analyse the proportion of attempts that were to non-rewarding holes. All models were checked for over-dispersion but no correction was needed (Hector, 2015).

For all analyses we used a model selection approach (Symonds and Moussalli, 2011) using the AICcmodavg package (Mazerolle, 2017, version 2.0-3) where candidate models included all possible combinations of trial number as a linear term (to indicate learning), age (adult or juvenile), learning sequence (LS1, LS2), and social category (social, semi-social or alone). We included interactions between trial number and age, trial number and learning sequence, and learning sequence and age, to assess if learning rates differed between age groups and between stages after hihi had experienced a change in reward hole cues. When averaging across models, those including interactions were treated separately to avoid over-estimating their effect (Mazerolle, 2017). Trial number was included as a random slope and individual identity as a random intercept in all models to account for repeated measures of the same individuals, as birds could have multiple trials. This also accounted for differences in individual learning rate. Models were ranked according to their corrected Akaike Information Criterion (AICc) with the number of individuals used as the sample size. Effect sizes (± 95% confidence intervals) were averaged from all models < 2 AICc units of the top-ranked model and used to assess the magnitude of each predictor variable's effect (Nakagawa and Cuthill, 2007; Symonds and Moussalli, 2011).

We also tested whether there was a pre-existing preference for black or white or for hole location, to understand how this may have affected foraging. We used a binomial sign test to compare the expected random probability of visiting a black hole (0.66, two out of three available holes was marked as black) with the observed hole visited by individuals during their first ever trial in the experiment. We then used a G-test for each age class to assess whether first holes attempted were randomly distributed to each of the three possible holes.

**Foraging duration of adult and juvenile hihi**

We analysed if differences in learning could have been affected by time spent in the feeder arena, and how the proportion of time spent feeding varied with age. We used GLMMs to analyse how three different variables changed between age groups. To understand foraging efficiency and learning opportunities, we analysed (i) the time spent in the feeder arena (with a Poisson error distribution) and (ii) the proportion of time spent feeding (with a binomial distribution). For both of these response variables we included age as a predictor variable. We then analysed (iii) the length of time between visits ("inter-trial interval") to explore if feeding behaviour changed after a longer interval (i.e. hihi became less likely to remember the feeder arrangement, or had higher feeding or sampling motivation). Here, we used two

further sets of GLMMs. The first modelled if the first hole hihi attempted on their return was the reward hole (yes = 1, 0 = no, binomial error distribution). The second modelled the number of non-reward holes attempted as the response variable (with a Poisson error distribution), to measure how much non-rewarding behaviour hihi made on return to the feeder arena. Both models included age and inter-trial interval as predictor variables, separately and in interaction. In all of these analyses, we included a random intercept term for individual identity to account for repeated trials by individuals. Again, all models were ranked by AICc and effect sizes were calculated from all models within 2 AICc units of the top-ranked model.

**Cue use**

We determined if hihi associated cues to locate the reward hole after each switch by comparing the distributions of the first hole attempted by each bird post-switch, to an expected random distribution of 33% in adults and juveniles. We also determined how hole use changed in the trials before and after each switch by comparing the distribution of holes attempted post-switch to the distribution of the last hole attempted prior to the switch. For both of these analyses, we used G-tests following previous analyses of cue use by Herborn and Healy (2011).

## *Results*

A total of 78 hihi visited the feeder arena across the duration of the experiment; this included almost all known adult males (*N* = 36, 100 %), juvenile males (*N* = 24, 92 %) and juvenile females (*N* = 16, 84%) recorded during that year's population census (Anderson, 2016), but only 2 adult females (from 21 known birds, adult female hihi rarely use supplementary feeders during this time (Anderson, 2016)). As our main comparison of interest was age, we therefore focussed on male hihi behaviour. Adult males ranged from 1 - 6 years old (56 % were first year adults, matching the population at large (Anderson, 2016). Overall, our sample of birds captured the majority of the population, and included a range of adult ages. Using males also meant possible sex-based differences in black and white cue preference would not affect learning (for example, due to biases based on plumage preferences between sexes).

### LEARNING TO LOCATE THE REWARD

Hihi showed evidence of learning as they became more likely to go to the rewarding hole first as trials progressed (trial number effect: 0.48±0.11, 95% CI = 0.27 – 0.70, Figure 2.2a; models excluding trial number had very little support: ΔAICc ≥ 36.24, Supplementary Table 2.1a) but juveniles always performed more poorly than adults (age effect: -0.70±0.30, 95% CI = -1.30 - -0.11). After the fourth trial, only three adults (8.3%) visited a non-rewarding hole first, while 14 juveniles (58.3%) continued to consistently make this error. However, looking only at the first hole attempted during each bird's first

trial, adults showed a preference for the white hole (chance of choosing white hole higher than random, $N = 34$, $P = 0.005$), while juveniles showed no bias ($N = 23$, $P = 0.51$). There was no bias towards hole location in adults or juveniles (adults: $N = 34$, $G = 3.64$, $P = 0.16$; juveniles: $N = 21$, $P = 0.10$). To assess whether this influenced differences in learning, we modelled effects of the colour of the first hole attempted on our measures of learning but found little evidence that the learning task was not equivalent for age classes across the rest of the experiment (included for comparison in Supplementary Table 2.1, as "colour of first hole attempted").

We next focussed on the number of holes hihi attempted as a measure of continued sampling, as both a total number of holes and the proportion of holes visited that were non-rewarding (Figure 2.2b, c; Supplementary Table 2.1). Hihi sampled fewer holes in total across trials, showing an increasing preference for visiting only the reward hole (trial number effect = -0.05±0.01, 95% CI = -0.07 – -0.03, Figure 2.2b). Despite age being included in two of the top-ranked models, overall there was little difference in the number of holes adults and juveniles sampled (age effect = 0.13±0.08, 95% CI = -0.03 – 0.29; Figure 2.2b). However, when sampling, juveniles were more likely to attempt non-rewarding holes compared to adults (age effect = 0. 62±0.21, 95% CI = 0.21 – 1.04, Figure 2.2c). This difference was not because juveniles were less likely to locate the reward hole on their first attempt, as the total number of holes attempted did not differ between age classes (see above). Taken together, these results show that hihi learned to locate the reward, although juveniles remained poorer at this than adults (Figure 2.2a). Hihi also became more likely to attempt only the rewarding hole over time, but juveniles continued to sample proportionally more non-rewarding holes (Figure 2.2b, c).

We expected that hihi that visited in both stages would become more familiar with the feeder arena, however in most analyses of learning there was a negligible effect of learning sequence (Supplementary Table 2.1). It was not included in models with $\Delta$AICc < 2 for first hole visited (Supplementary Table 2.1a), and showed no effect for the total number of holes visited, and proportion of non-rewarding holes, despite being included in the top model sets (total holes: age*learning sequence effect = -0.22±0.17, 95% CI = -0.56 – 0.11; learning sequence effect = -0.11±0.08, 95% CI = -0.26 – 0.05; Supplementary Table 2.1b; proportion non-rewarding holes: trial number*learning sequence effect = -0.17±0.1, 95% CI = -0.36 – 0.02; Supplementary Table 2.1c). Finally, social category had no effect (Supplementary Table 2.1).

**FORAGING DURATION OF ADULT AND JUVENILE HIHI**

Both juvenile and adult hihi spent the same proportion of time feeding at the reward hole while in the feeder arena: the null model analysing proportion of time spent feeding was ranked higher than one containing age as a parameter (effect of age on feeding proportion = -0.42±0.36, 95% CI = -1.14 – 0.29; Figure 2.3a; Supplementary Table 2.2a). However, juveniles spent longer in the feeding arena overall compared to adults (effect of age on time in feeding arena = 0.34±0.14, 95% CI = 0.06 – 0.62, Figure

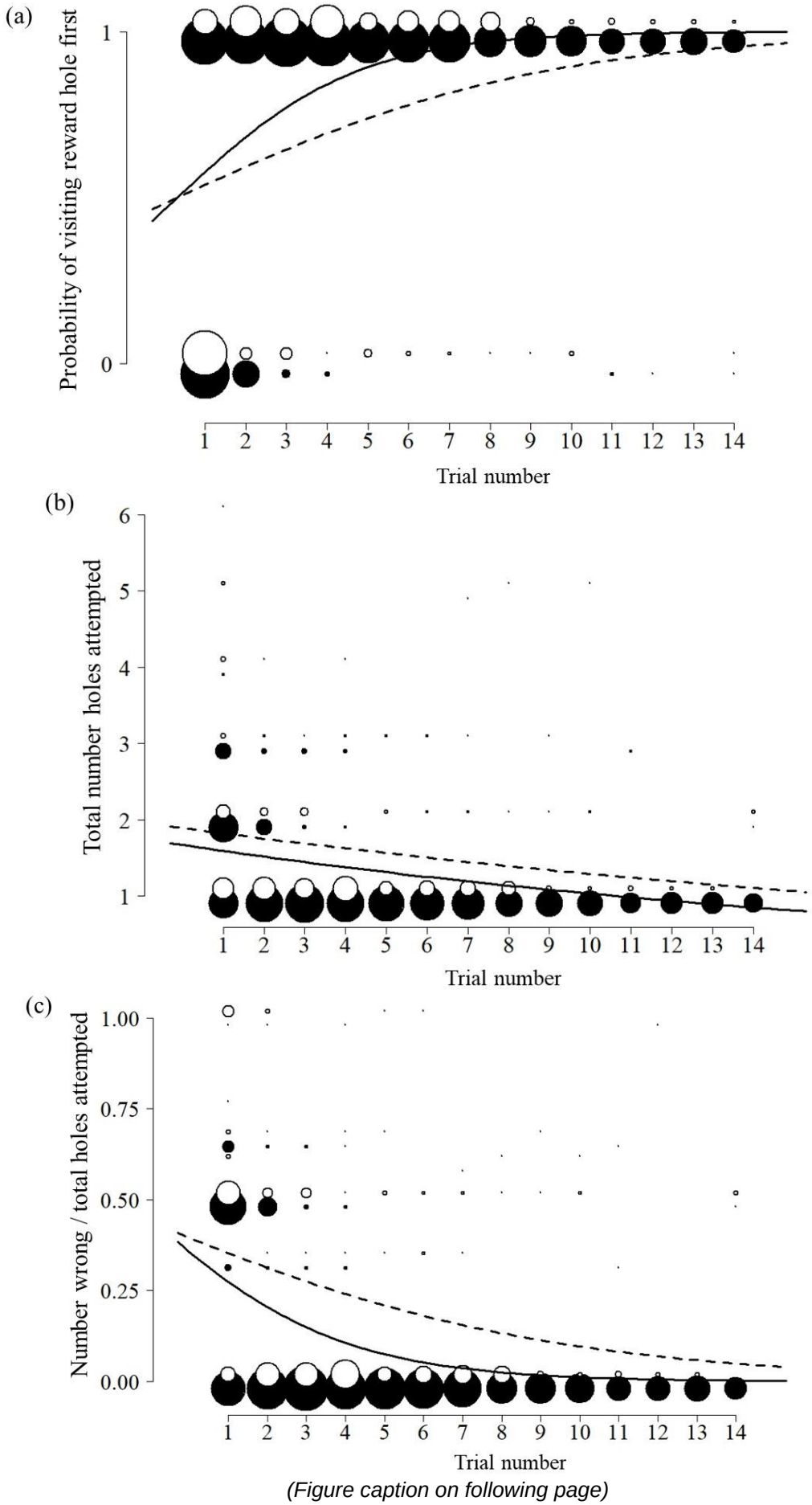
2.3b; Supplementary Table 2.2b). This suggested that, although juveniles had more opportunity to learn about the feeding task, they still had poorer foraging efficiency and needed to compensate by foraging for longer. Regardless of age, hihi were less likely to visit the reward hole first if they had been away for a longer inter-trial interval, and sampled more non-rewarding holes (effect of absence time on likelihood of visiting reward hole first = -0.36±0.08, 95% CI = -0.51 – -0.20, Supplementary Table 2.3a; effect of absence time on number of non-rewarding holes = 0.39±0.06, 95% CI = 0.27 – 0.51, Supplementary Table 2.3b). Although juveniles spent longer away on average than adults (effect of age on inter-trial interval = 0.81±0.36, 95% CI = 0.10 – 0.52, Supplementary Table 2.3c), juveniles that were absent the longest actually sampled from fewer non-rewarding holes in total than adults (effect of inter-trial interval*age on number of wrong holes sampled: -0.26±0.08, 95% CI = -0.41 - -0.11, Figure 2.3c, Supplementary Table 2.3b). Therefore, these results suggest the differences in juvenile and adult learning were not only an effect of juveniles having less opportunity to learn or more time to forget.

**CUE USE BY ADULT AND JUVENILE HIHI**

After moving the location (but not the colour cue) of the reward in Switch 1 (Figure 2.1c), we found some evidence that adults and juveniles were using cues differently to locate food (Figure 2.4a). Only a quarter of juveniles (5/17) followed the colour cue to feed from hole B, while the majority (10/17) continued to attempt the location that provided food in Stage 1 (pre- vs. post-Switch 1 hole preference: $G$ = 4.48, $P$ = 0.11, Figure 2.4a). Two chose hole c which had not been rewarding and was marked black. Adults, on the other hand, changed their behaviour (pre- vs. post-switch, $G$ = 9.77, $P$ = 0.008): while 8/18 birds continued to feed from hole a (now marked by a black circle), 7/18 followed the colour cue (3/18 chose hole c). As the proportions of adults and juveniles following the colour cue were small, however, there was no significant difference between the ages in their cue preference post-switch ($G$ = 3.57, $P$ = 0.17).

The difference in cue use between adults and juveniles became more pronounced after Switch 2. Adults now clearly used the colour cue more than juveniles as post-switch preferences differed depending on age (post-switch juvenile vs post-switch adult: $G$ = 13.02, $P$ = 0.002, Figure 2.4b). Most adults favoured the hole marked with the white circle (12/16 birds, $G$ = 13.02, $P$ = 0.002). Juveniles' hole preference, on the other hand, was random ($G$ = 3.60, $P$ = 0.17): 5/17 returned to the location that was rewarding in Stage 2, 9/17 attempted the hole marked with the white circle, and 3/17 attempted to feed from the alternative hole that had neither the white cue nor had been the previously-rewarded location. Separating the colour cue from the reward hole during Switch 2 also confirmed that hihi were learning cues and not simply detecting which hole was open; the rewarding hole was not favoured by a majority of either adults or juveniles in Stage 3 (Figure 2.4b). There was a trend for individuals that used the colour cue before the switch to be more likely to continue to follow this cue after the second switch than birds that first relied on location, although this was not statistically significant at $P$ = 0.05 (before and after comparison of cues used, McNemar chi-squared test: N = 33, $X^2_1$ = 3.5, $P$ = 0.061).

Regardless of which cue was used after either switch, most hihi subsequently adjusted their behaviour and relocated food by their third trial at the feeder arena (Switch 1: mean = after 1.72 ± 0.16 trials; Switch 2: after 1.93 ± 0.17 trials). There was no difference between adults and juveniles in the number of trials it took before they went straight to the rewarding hole (Wilcoxon rank sum test, Switch 1: $W = 95$, $P = 0.60$; Switch 2: $W = 98$, $P = 0.40$). Finally, the number of trials made during the stage prior to cues being switched did not predict which hole was chosen first following the switch (Switch 1: Kruskal-Wallis rank sum test, $X^2_{15} = 18.99$, $P = 0.21$; Switch 2: Kruskal-Wallis rank sum test, $X^2_{14} = 8.74$, $P = 0.85$). This shows that the differences in hole preferences we detected were unlikely to be a result of different levels of experience of the feeder arena.




*(Figure caption on following page)*

**Figure 2.2.** Feeder holes attempted by adult (closed circles, solid line) and juvenile (open circles, dotted line) hihi over trials at the arena (*N* = 60 individuals). (a) Probability that the rewarding hole was chosen first, (b) total number of holes attempted during each trial, and (c) proportion of holes attempted that were non-rewarding. All points are scaled to the number of individuals they represent (maximum number of individuals: (a) 28; (b) 25; (c) 26). Lines of best fit come from the relevant top-ranked models (see Supplementary Table 2.1).

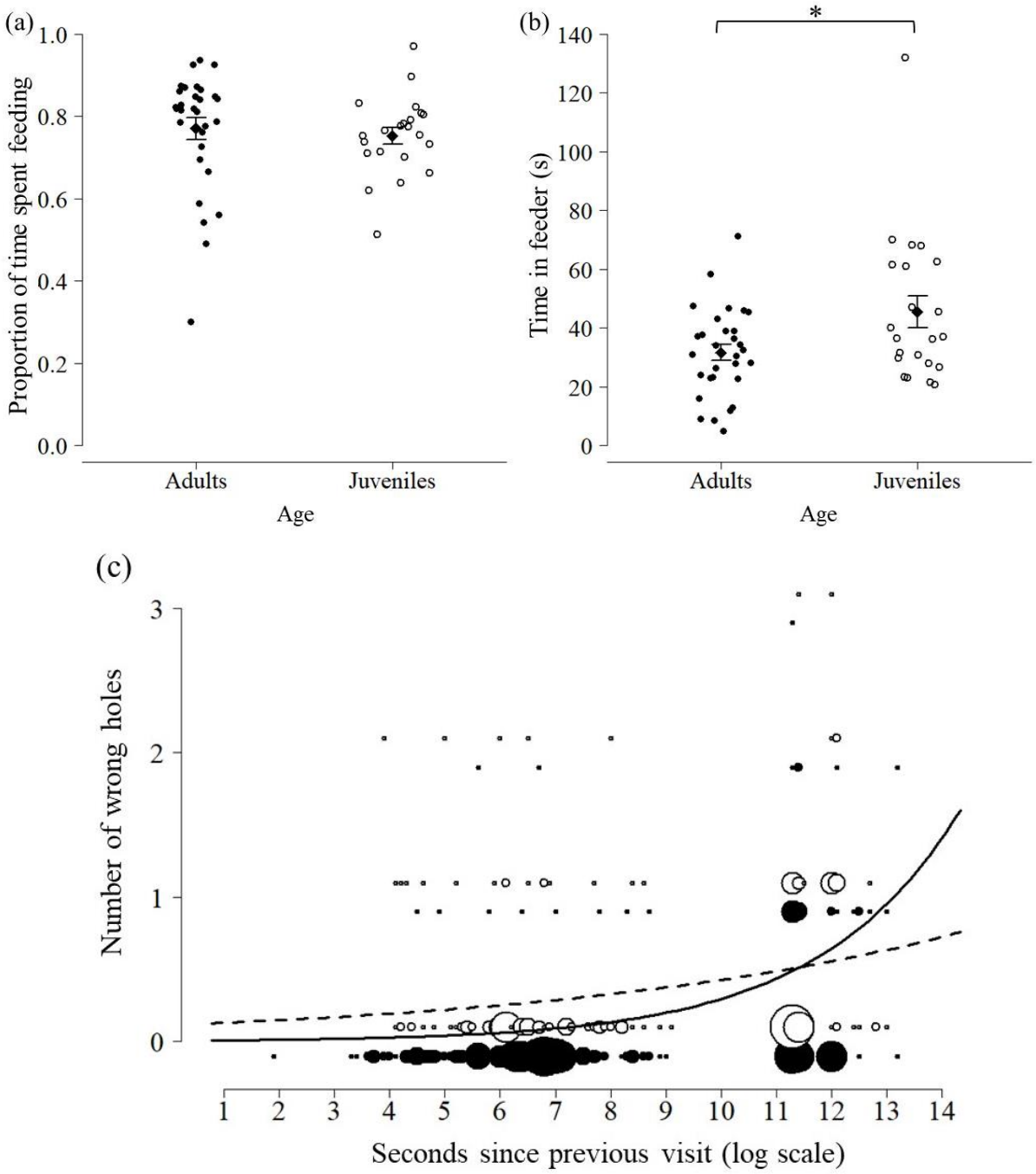



**Figure 2.3.** Effects of time on aspects of feeding behaviour in adult and juvenile hihi (*N* = 60). (a) Proportion of time adult (closed circles) and juvenile (open circles) hihi spent feeding at the reward hole; (b) Length of time adult (closed circles) and juvenile (open circles) hihi spent in the feeder arena. Asterisk indicates that the time spent in the feeding arena was significantly different between adults and juveniles (see Results). For (a) and (b), mean and standard error indicated by closed diamonds and capped lines. Points jittered by 3 on the x-axis to improve visibility; (c) number of wrong holes attempted by adults (closed circles, solid line) and juveniles (open circles, dotted line) on their return to the feeder arena, depending on the length of time since their previous visit (inter-trial interval). Points are scaled to the number of individuals they represent (maximum point size = 10 individuals). Lines of best fit come from the top-ranked model (Supplementary Table 2.3b). Please note time is plotted on a log-scale: as this experiment was conducted over days, hihi could have inter-trial intervals overnight (the gap at log10 covers this overnight period).

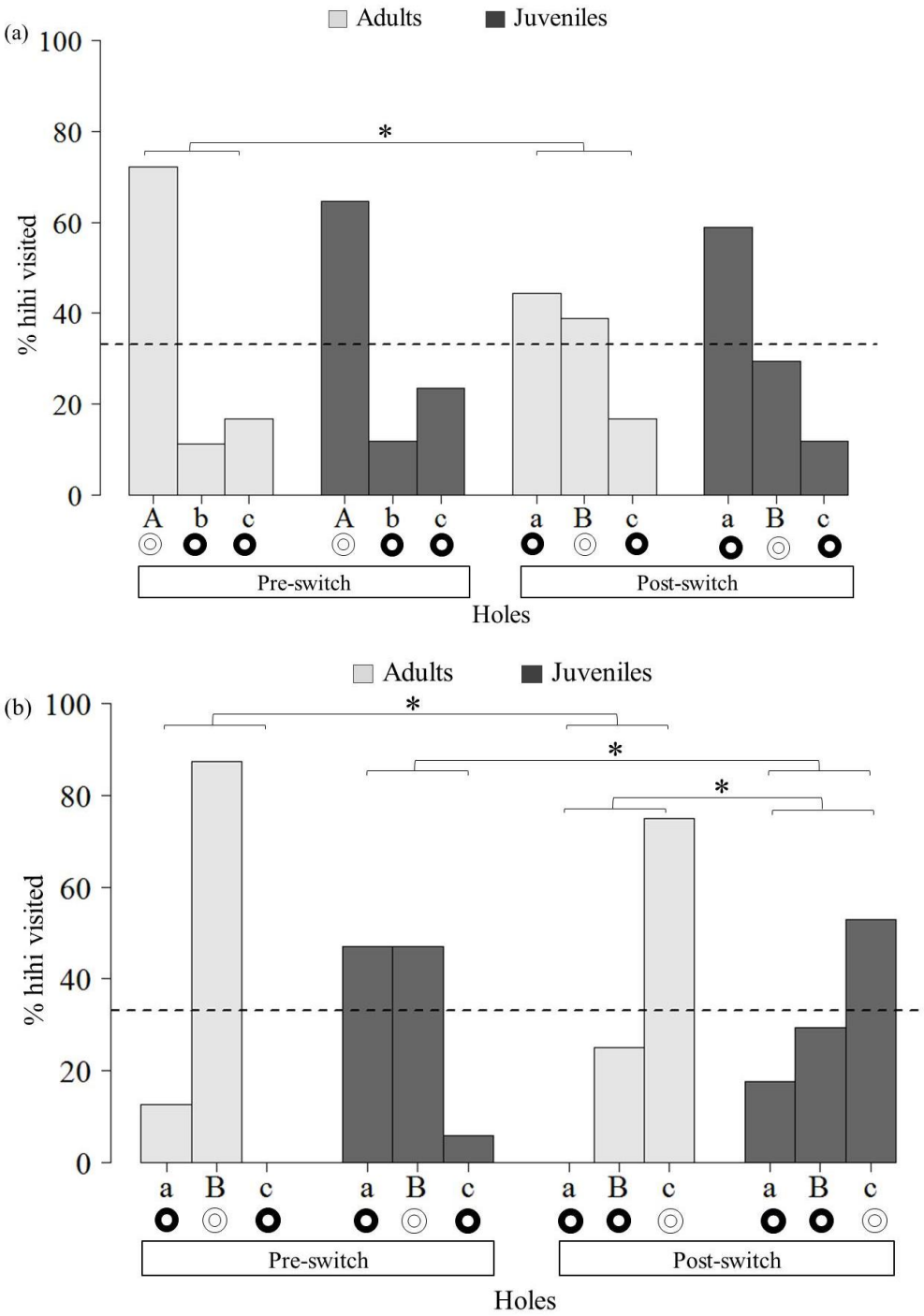



**Figure 2.4.** First hole attempted by adult (light grey) and juvenile (dark grey) hihi during trials before and after a switch. (a) Holes attempted by adults (*N* = 18) and juveniles (*N* = 17) before and after Switch 1, and (b) before and after Switch 2 (adults: *N* = 16, juveniles: *N* = 17). Hole marking corresponds to Figure 2.1c, where capitalised letters indicate rewarding holes and symbols indicate colour cue. Dashed line represents no preference (random distribution), and asterisks indicate significantly different distributions (using G-tests, see Results for details).

## *Discussion*

Associating cues with food rewards is well-known across the animal kingdom, but it remains less clear whether age affects cue use and learning in the wild. Our experiment shows that hihi, a generalist nectarivore, also learn to locate new food sources: both adult and juvenile hihi became more likely to attempt the reward location first over repeated trials. However, juveniles were less likely to attempt the reward first compared to adults. They also continued to sample non-rewarding holes more than adults, even after they had located the food reward; this may explain why juveniles spent longer feeding across trials. Although adults showed some pre-existing bias for the white hole, juveniles did not seem to compensate for initial differences during learning: they remained more likely to sample non-rewarding holes even with experience, and as the reward moved during the experiment, adults appeared to follow the colour cue more than juveniles did (20% fewer juveniles followed the colour cue than adults after the final switch of the experiment). This suggests that more juveniles may have relied on location while adults favoured the colour cue, but juveniles also continued to sample the environment more than adults. Thus: why do learning patterns change with age, and what are the consequences?

There are two possible explanations: juveniles may learn more slowly than adults to use cues to find food (Thornton and Lukas, 2012), or they may be using a different foraging strategy (Krebs, Kacelnik and Taylor, 1978; Krebs and Inman, 1992). If poorer learning is responsible for greater sampling by juveniles, this may be due to continuing musculoskeletal or neurological growth and maturation, and a lack of experience interacting with environmental stimuli (Marchetti and Price, 1989; Healy and Hurly, 2004). In macaques (*Macaca mulatta)*, a lower performance at set-shifting tasks in juveniles compared to adults has been attributed to a less developed prefrontal cortex (Weed, Bryant and Perry, 2008), and similarities with analogous regions of the avian brain (Timmermans *et al.*, 2000; Olkowicz *et al.*, 2016) could suggest that the development of these areas is also important for cognition in birds. Although our learning task was novel for both adults and juveniles, by virtue of their age adults are likely to have interacted with more cues in general. Adults' accumulated experience could make them better able to assess a range of cues, respond appropriately (Mery and Burns, 2010), and select higher-gain patches than juveniles when foraging (Gass and Sutherland, 1985; Whitfield, Kohler and Nicolson, 2014), even in novel environments. While juvenile foraging efficiency may improve with experience, acquiring this experience can be a slow process with many opportunities to make mistakes along the way.

On the other hand, flexible sampling by juveniles may help them keep an updated picture of their environment so they can forage optimally in the current conditions (Krebs, Kacelnik and Taylor, 1978; Krebs and Inman, 1992). In captive studies in baboons (*Papio papio*), behavioural flexibility helped juveniles reverse behaviour faster than adults (Bonté, Kemp and Fagot, 2014). In the wild, this may be adaptive because in many species (including hihi (Craig, 1985)), juveniles are subordinate to adults

(Dingemanse and De Goede, 2004; Verhulst *et al.*, 2014). If juveniles have fewer opportunities to feed at high-quality food patches due to both contest and exploitation competition (Sol *et al.*, 1998) having up-to-date knowledge from diverse foraging sites could help them make use of a variety opportunities when displaced (Keynan, Ridley and Lotem, 2016). Sampling may also allow juveniles to compensate for using the wrong cue, and allow them to locate rewarding patches more quickly. This explore and exploit strategy (Krebs, Kacelnik and Taylor, 1978) could explain why we found no difference in the number of trials that it took adults and juveniles to re-locate the reward hole after it was moved, despite initial differences in their cue use. However, sampling also incurs costs when moving between patches (in both time budget allocation and energy expenditure) (Bryan, Coulter and Pennycuick, 1995; Stephens, Brown and Ydenberg, 2007), and continuing to sample patches of no gain in case they later become rewarding may lead juveniles to waste energy. In our experiment, we found that juvenile hihi had to forage for longer than adults to reach the same level of reward intake, which may demonstrate how a sampling strategy may be costly to young hihi in terms of time budgeting, especially when they have lower chances of locating food to begin with. Therefore, determining if sampling by juveniles is actually adaptive requires further work, to understand if the costs of less efficient foraging are offset in other ways, or whether this gives one reason why juveniles, especially for birds, often have low survival (Naef-Daenzer and Grüebler, 2016).

How might our findings help hihi? The majority (six out of seven) of extant hihi populations have been established through translocations and are supplementary fed as a crucial part of their management (Chauvenet *et al.*, 2012). Supplementary feeding is often used in conservation of vulnerable populations in other taxa, with conservation biologists calling for integration of nutritional and population ecology to provide the most effective management (Ewen *et al.*, 2015). Our findings suggest the cognitive ecology of the species being helped should also be considered to inform management practices. For example, the locations of feeding stations at managed hihi sites are sometimes changed, or even redesigned, for logistical reasons. Avoiding modifying feeder locations or establishing new feeding sites when juveniles are newly independent may give juveniles the best chances of learning appropriate cues and enable them to access food easily in the future. Cues may also need to be considered in other contexts, such as selecting nest sites (Seppänen *et al.*, 2011). As nest boxes are also used in some hihi populations, it would be interesting to test if we can manipulate cues to help hihi locate new nesting sites.

In summary, we found that both age classes learned to locate a food reward, but juveniles continued to sample foraging options more than adults and spent longer foraging overall. The range of cues used by each may have differed; adults were more likely to follow a colour cue whereas juveniles relied on location. Our study helps highlight that learning strategies change with age, and that young animals may be disadvantaged in several ways when compared to adults: they have had less opportunity to learn and generalise cues, and may not use the most efficient foraging strategies. Understanding how young animals use different sources of information to inform learning may help explain why some reach adulthood, while others do not.

# CHAPTER 3

# One of the gang: social group dynamics in juvenile hihi

*I gratefully acknowledge Donal Smith and Mhairi McCready for monitoring hihi breeding seasons and Marcus Rowcliffe for advice on multistate analysis*

Living in groups comes with many potential benefits, especially for juveniles. Naïve individuals may learn how to forage, or avoid predators through group vigilance. Understanding these benefits, however, requires an appreciation of the opportunities juveniles have to associate with (and learn from) others. Here we describe social groups in terms of residency, movement, relatedness, and social associations from the perspective of juvenile hihi, a threatened New Zealand passerine bird. Over three years, we identified individuals in groups, their relatedness, and behavioural interactions. Using multistate analysis, we compared movement and residency of adults and juveniles and found that groups were composed predominately of juveniles which remained at group sites for longer than more transient adults. Movement of juveniles between groups did occur but was generally low. There was no evidence that siblings and parents were likely to be seen in groups together. With an initial understanding of group structure, we next asked what characteristics predicted assortment in social network associations. By identifying groups of co-occurring juveniles from time-stamped observations of individual hihi and building a social network, we found that juveniles were most likely to associate with other juveniles. Associations were also predominantly based on locations where hihi spent the most time, reflecting limited movement among separate groups. We suggest groups are best described as “gangs” where young hihi have little interaction with adults. These spatially-separated groups of juveniles may have consequences for social information use during the first few months of independence in young birds.

## *Introduction*

Social groups are found across the animal kingdom (Ward and Webster, 2016). Generally, group living is thought to provide advantages such as better foraging opportunities if groups can collectively out-compete other more dominant animals, and protection from predators through shared vigilance (Rubenstein, 1978; Molvar and Bowyer, 1994; Gompper, 1996; Hass and Valenzuela, 2002; Le Bohec, Gauthier-Clerc and Le Maho, 2005). Sociality may benefit juveniles in particular, as they are inexperienced compared to adults (Galef and Laland, 2005) and can be less adept at finding food (Sullivan, 1989; Lind and Welsh, 1994; Franks and Thorogood, 2018) or avoiding predators by themselves (Naef-Daenzer, Widmer and Nuber, 2001). Therefore, juveniles may be able to use information from others in groups ("social information") to reduce their uncertainty about how best to behave (Dall *et al.*, 2005). However, who juveniles encounter in groups will affect the opportunities they have to learn socially (Seppänen *et al.*, 2007; Krause *et al.*, 2015), along with additionally impacting on other consequences of group living such as risk of contracting disease (Godfrey *et al.*, 2009; Drewe, 2010). Therefore, the dynamics of groups (where groups form, when they form, and which individuals group) need to be quantified to understand why animals are social, especially juveniles (Krause and Ruxton, 2002; Ward and Webster, 2016).

In young wild birds, there are examples of three types of groups which vary in age structure, relatedness structure, and site stability. Firstly, birds are well-known to form mobile foraging units or "flocks", with no particular structure by relatedness or age (so are not unique to juveniles) (Morse, 1978; Saitou, 1978, 1979; Ekman, 1989; Templeton *et al.*, 2012). All group members can access ephemeral food sources as the group moves across an environment, and they also share costs of predator vigilance (Rubenstein, 1978; Molvar and Bowyer, 1994; Hass and Valenzuela, 2002; Sutton, Hoskins and Arnould, 2015). Secondly, juveniles can form groups without adults, such as "gangs" in ravens (*Corvus corax*) (Dall and Wright, 2009). Gangs are similar to flocks in that their main function is to access ephemeral food resources; however, gangs operate around stable roosting sites which act as information centres (Dall and Wright, 2009) and also allow juveniles to out-compete more dominant adults (Wright, Stone and Brown, 2003; Ward and Zahavi, 2008; Dall and Wright, 2009). Thirdly, juveniles may form stable congregations as "crèches". These groups contrast with gangs or flocks because crèches form before juveniles become fully independent from parents, and serve to promote juvenile survival as parents actively care for their young with food provisioning and vigilance (Balda and Balda, 1978; Marzluff and Balda, 1992; Clayton and Emery, 2007). Despite group structure being a crucial part of the social environment of juveniles, little is known outside of these examples. Overall, juvenile behaviour is understudied in general, especially in birds (Templeton *et al.*, 2012).

One way groups may help juveniles overcome their naivety is by providing opportunities to learn rapidly when interacting with group members (Coussi-Korbel and Fragaszy, 1995; Krause and Ruxton, 2002). If groups are comprised of different age classes, or individuals that use the environment in different ways, juveniles may encounter a range of potential social information (Seppänen *et al.*, 2007; Pinter-Wollman *et al.*, 2013). For example, juveniles in flocks encounter both experienced adults and other juveniles, so information about ephemeral food sources can be shared among group members ("oblique" and "horizontal" transmission, respectively (van Schaik, 2010)). In gangs where associations are between juveniles only, interactions can include "social play", documented in species such as ravens (Heinrich and Smolker, 1998). "Play" behaviours in animals are notoriously difficult to define (Bekoff and Allen, 1998) but generally "social play" involves at least two individuals engaged in a reciprocated behaviour who alternate between roles (Diamond and Bond, 2003). During such play, information may be shared among participating individuals (Diamond and Bond, 2003). However, the presence of many naïve individuals in gangs could increase the risk of associating with misinformed peers, especially if some individuals are more social than others (Pruitt *et al.*, 2016). Across the animal kingdom, genetically-related groups such as crèches promote associations between parents and offspring (Balda and Balda, 1978; Clayton and Emery, 2007) that allow for learning (e.g. European shags *Phalacrocorax aristotelis*: Velando, 2001; ravens *Corvus corax:* Schwab *et al.*, 2008; vervet monkeys *Chlorocebus pygerythrus:* van de Waal, Bshary and Whiten, 2014) and can even facilitate teaching (e.g. meerkats *Suricata suricatta* (Thornton, 2006; Thornton and Raihani, 2010)). Alternately, some studies suggest associations with non-kin can still be beneficial when they may have a different range of experiences (Hatch and Lefebvre, 1997). Describing group structures and associations should therefore help us to understand the benefits of group living for juveniles more clearly (Sih, Hanser and McHugh, 2009).

Analysing group behaviour in space and time can quantify broad-scale consistencies to show who groups, when and where. However, it does not fully capture how individuals interact as a consequence of group structure. Social network analysis can overcome this problem (Wey *et al.*, 2008); animals form social networks through non-random preferred and avoided associations which can be quantified and analysed statistically (Krause and Ruxton, 2002; Krause, Lusseau and James, 2009; Sih, Hanser and McHugh, 2009; Krause *et al.*, 2015). Therefore, here we first used a form of re-sighting analysis to consider movement, residency and relatedness in groups of juvenile and adult birds. We then compiled social networks to investigate how movement, residency and relatedness affected associations. Finally, we observed interactions between individuals to understand how these may influence information sharing. Our study species was the hihi (*Notiomystis cincta*), an endemic New Zealand passerine. Hihi provide a good example where juveniles are known anecdotally to form groups during early life, although these have not been studied systematically before. We aimed, therefore, to describe group formation and membership, compare them to juvenile groups in other species, and understand how group characteristics affected associations (Table 3.1). If hihi groups were crèches, we predicted both adults (parents) and juveniles (siblings) to be consistently sighted together in groups. However, we would expect different structure if groups were gangs (juveniles should be present much more than adults) or flocks (individuals would not remain in one site; adults and juveniles would be present but unrelated).

**Table 3.1.** Predictions for group structure and social associations for juvenile hihi, with reference to previously-described groups of birds. All group types can be compared to a "null" unstructured group of randomly-associating individuals.

| **Group characteristics** | **Group type** | | | |
|---|---|---|---|---|
| | **Flock** (Saitou 1978; 1979) | **Gang** (Marzluff et al., 1996) | **Crèche** (Marzluff & Balda 1992) | **Null** |
| (1) Age composition:<br>Juveniles are more resident in groups than adults<br>• Juveniles re-sighted more days than adults;<br>• Age structures associations<br>• Juveniles interact | No | Yes | No | No |
| (2) Spatial structure:<br>Juveniles group in consistent locations<br>• Low movement between separate groups;<br>• Location structures associations | No | Yes | Yes | No |
| (3) Relatedness:<br>Groups contain parents and offspring<br>• Juveniles consistently sighted with parents/siblings;<br>• Relatedness structures associations | No | No | Yes | No |
| (4) Groups random (across/within years) | No | No | No | Yes |

## *Methods*

### STUDY POPULATION

Our study was conducted over three years (2015 – 2017) on Tiritiri Matangi Island (Auckland, New Zealand, 36°36'00.7"S 174°53'21.7"E), between January – April when juvenile hihi (birds in their first year) had fledged and dispersed from nests. This 2.5km$^2$ island is characterised by a central longitudinal ridge (60-80m altitude) with a series of latitudinal ridges and gullies on either side covered in a mixture of original and replanted native bush. Supplementary sugar water feeders are provided year-round for hihi at five sites across the island. This is a closed population with no immigration or emigration (except through birth and mortality) and all individuals are uniquely identifiable from coloured leg ring combinations. The population varied between 180 and 270 individuals over the three years, with similar proportions of juveniles and adults (second year or older) each year (Smith and Ewen, 2015; McCready and Ewen, 2016, 2017). Every year, all breeding attempts are monitored and identities of breeding pairs recorded. During this study, parentage was assigned as part of the monitoring of each breeding season, by visually identifying the adult male and female hihi present throughout nest building, egg laying and chick care. All chicks hatched in the same nestbox were assumed to be siblings. Although there is

variable extra-pair paternity in hihi (Ewen, Armstrong and Lambert, 1999; Brekke *et al.*, 2013), all nest-mates were most likely to be at least maternal-siblings (there is no evidence of conspecific brood parasitism in hihi) and the social male cares for the offspring in his nest (Ewen and Armstrong, 2000). The first year of our study (2015) was a poorer breeding season than 2016 and 2017 (2015: 89 fledglings; 2016: 132 fledglings; 2017: 151 fledglings); thus, we accounted for year in any analyses using combined data.

**DETECTING GROUPS**

Each year, we surveyed for groups between January – February in spatially-separated areas of forest habitat. In 2016 and 2017, we increased the search area to ensure no other potential groups were missed. The numbers of unique juveniles were recorded for one hour in each location, and group sites were assigned after two weeks if we saw at least three juveniles during more than 80% of 10 surveys per location. We further confirmed that there were no other sites with higher numbers of juveniles during the annual February census of the population, which is conducted every year by trained conservation staff who survey the entire island over 40 hours. We then continued to survey group locations from February – April, using one-hour surveys divided into 30-second time blocks (one survey = 120 blocks). Within each block we recorded the identity of all hihi (both juvenile and adult) perched within a 10-metre radius of the observer. We recorded individuals present across blocks to determine presence to the nearest 30 seconds. All observations were made with binoculars (Zeiss Conquest® HD 8x42) by one observer (VF). In total we recorded 15 hours per group site in 2015, and 25 hours per site in 2016 and 2017; surveys were distributed evenly across the three months.

During each 30-second block, we also recorded the occurrence of behavioural interactions and the identities of the individuals they involved (Table 3.2; Figure 3.1). Interactions were classed as “directed” if there were clear initiators. However, some behaviours were not clearly initiated by any particular individual, so we classified these as “undirected” (Table 3.2). One such undirected behaviour was defined as “playfight”; *sensu* definitions by Bekoff and Allen (1998), and Diamond and Bond (2003). Playfighting involved at least two interacting individuals, and included actions derived from antagonistic behaviour (pecking at others) but which caused no observable injury and showed no clear outcome (the attacker could then become the attacked). However, we accept this behaviour may need to be further investigated in future to support the use of a term including “play”.

**Table 3.2.** Ethogram of common interactions observed between juveniles in groups, and their definitions.

| | Interaction | Description |
|---|---|---|
| Directed behaviours | Chase | Individual moves towards another perched hihi, displaces it, and then continues moving in the same direction as the second bird. |
| | Chased | Individual moves away from its original perch after another hihi has initiated moving towards the focal individual |
| | Follow | Individual leaves a perch to move in same direction as another hihi that moves off before focal individual. |
| | Followed | Individual leaves a perch before another perched bird, and the second bird moves off in the same direction as the focal individual. |
| Undirected behaviours | Huddle | Two or more birds perch touching side-by-side and do not move from position on perch. May include allopreening. |
| | Playfight | Two or more birds perch touching side-by-side, then peck at each other, hang up-side down on branch, shuffle next to each other along branch. |

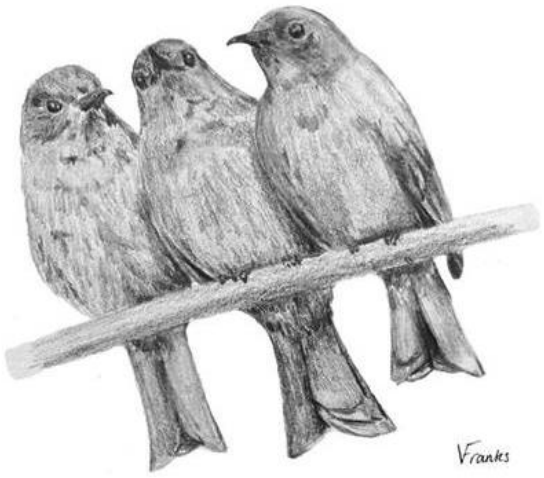



**Figure 3.1.** Sketch of huddle behaviour, with three juvenile hihi perching side-by-side on a branch.

## DATA ANALYSIS

### Re-sighting and movement analysis

We first used a multistate approach in Program MARK (version 9.0) (White and Burnham, 1999) to understand residency in group sites and movement between sites for juveniles and adults. Multistate analyses estimate survival ($S$) and re-sighting ($\rho$) of identifiable individuals of different "states" from repeated sightings across replicated surveys, along with likelihood of movement between states ($\psi$) (White, Kendall and Barker, 2006). Survival and re-sighting are often inherently linked and considered together to investigate population dynamics (i.e. to identify true mortality instead of absence of

detection). However, in our study we used these three parameters in a novel way to determine different patterns of hihi group structure. We assumed mortality was constant over our short study periods each year (Jolly, 1982), supported by previous studies of adult and juvenile survival in this population (Low and Pärt, 2009). Including varying survival by age in preliminary exploratory models also indicated low mortality (98-99% survival each year for both ages across all observational surveys; results not presented) suggesting birds were alive throughout the study period. We could then use $\rho$ to quantify presence/absence in groups (larger values of $\rho$ indicated high residence within groups as opposed to independent living), and track movement between groups using state transitions (higher values of $\psi$ indicating greater movement between known groups). In 2016 we verified that our survey method was reliable (Appendix 2.1) to be confident in estimating $\rho$.

We constructed re-sighting histories for each bird seen each year to represent if, and in which group, it was seen. Different groups were not surveyed at the same time (due to one observer), so we combined surveys together to create occasions that represented every group site. There was a maximum of two days between combined surveys to limit movement between groups within a survey occasion; if this did occur, we took the newest site as the site of residence for that individual in that occasion to account for movement (this occurred rarely: 2015 = 1/656 re-sightings; 2016 = 9/1974 re-sightings; 2017 = 7/3180 re-sightings). Thus, there were 8 survey occasions in 2015, 14 in 2016, and 20 in 2017. An example re-sighting history for one individual in 2015 is “aa0abbbb”, where the bird was seen in group “a” in survey occasions 1 and 2, not seen in survey occasion 3, seen in group “a” in survey occasion 4, and seen in group “b” for the remainder of survey occasions. We also specified if an individual was juvenile or adult with its re-sighting history. Therefore, our general starting model using our encounter histories in all three years was:

$$\boldsymbol{S(.)\ \rho(\text{age*survey occasion})\ \psi(\text{age + group})}$$

Here, we quantified different residency in groups between adults and juveniles by assessing if re-sighting $\rho$ varied across each survey occasion and between age groups, and if movement $\psi$ between groups also varied with age. For $\psi$, we specified group differences as varying distance and topology between groups could affect likelihood of moving between each group (Martin *et al.*, 2006; Strandburg-Peshkin *et al.*, 2017). Finally, different intervals between survey occasions were accounted for so likelihoods were not confounded by time.

Assessing fit allows for accurate inference from more reduced models (Burnham and Anderson, 2002; Cam *et al.*, 2004; Martin *et al.*, 2006). Therefore we assessed goodness-of-fit (GOF) of our starting models each year using median ĉ (variance inflation factor, a measure of overdispersion), which is generated by assessing the distribution of model deviances (White and Burnham, 1999; Gath, 2017). Values of median ĉ > 1 suggest overdispersion that needs to be corrected for in analyses while values > 4 suggest a structural failure of the general model (Burnham and Anderson, 2002). Each year, there were low levels of overdispersion (median ĉ: 2015 = 1.51; 2016 = 1.39; 2017 = 1.72) so we used the value of median ĉ as a correction factor for all further multistate analyses.

For each year, we constructed sets of models with all possible combinations of $\rho$ and $\psi$ parameters and ranked these by their corrected Quasi-Akaike Information Criterion (QAICc) values. AICc values represent the change in fit in comparison to the top-ranked model, and QAICc is used when ĉ is corrected following GOF testing. Any model < 2 QAICc units from the top-ranked model were considered equally well-supported. We also calculated QAICc weights for each model based on change in QAICc value from top-ranked model, which gave the relative likelihood that it was the most appropriate model (Burnham and Anderson, 2002). Any parameters included in models with QAICc weight > 0.00 were included in model-averaging to calculate effect sizes and 95% confidence intervals. Any parameter with a confidence interval that did not include 0.00 was considered to have a significant effect.

All further analyses were conducted in R (version 3.5.0) (R Core Team, 2017). To determine if juveniles were using the same group sites as their parents and maternal-siblings, using each juvenile's re-sighting history we calculated, per bird, the proportion of occasions it was seen in the same group as either of its parents, and the proportion of occasions it was seen in the same group as its maternal-siblings. We excluded any juveniles seen in one survey only as we could not calculate a proportion for these (*N*: 2015 = 10; 2016 = 18; 2017 = 10). When calculating proportions of time spent with maternal-siblings we also excluded any juveniles from single-fledgling nests or those with no maternal-siblings seen during our surveys (which may have died after fledging) (*N*: 2015 = 7; 2016 = 10; 2017 = 8). We assessed if juveniles that grouped closer to their nest-of-origin were more likely to co-occur with their maternal-siblings. We used a binomial Generalised Linear Model (GLM) where proportion of surveys with maternal-siblings was the response variable; using a proportion meant we could analyse all years together. Our predictors were proximity to nest-of-origin (distance to nearest 50m from group site to nest-of-origin, measured using Google Maps), number of surveys to ensure co-occurrence with maternal-siblings was not due to sampling bias, and year of survey (2015, 2016, 2017) to compare patterns among years. We constructed a set of candidate models including all combinations of predictors and ranked models by their AICc values. For any model < 2 AICc units larger than the top-ranked model, we calculated averaged effect sizes (±95% confidence intervals) for predictors using the package AICcmodavg (version 2.1-1) (Mazerolle, 2017). Based on the evidence from this initial exploration (see Results) we did not analyse effects of relatedness further using MARK, or in social network analysis.

**Social network analysis**

We constructed a social network for each year separately using the R package asnipe (version 1.1.9) (Farine, 2013). First we used the "gmmevents" function to detect temporal clusters in our time-stamped (to within 30s) sightings data and build an association matrix (Farine, 2013; Psorakis *et al.*, 2015). Using this approach avoids artificially restricted associations, which can occur using a more fixed time-window approach (Psorakis *et al.*, 2015). To validate if "gmmevents" groups represented true associations, we then compared the length of time (number of sequential observation blocks) we re-sighted hihi during observations to event lengths generated by "gmmevents". All networks were weighted, which incorporates both the number and strength of social connections and are considered more robust than

binary networks (Farine, 2014). Any hihi with fewer than 3 observation records were not included in networks (juvenile *N*: 2015 = 6; 2016 = 1; 2017 = 4; adult *N*: 2015 = 12; 2016 = 8 2017 = 7), to avoid a sampling bias that could affect network metrics (following the example of Aplin *et al.* (2012)).

As network data is not independent and thus violates the assumptions of many statistical tests, we compared observed networks to randomised networks as a null model to test hypotheses (Croft *et al.*, 2011; Farine and Whitehead, 2015; Farine, 2017). All randomised networks were generated using permutations of the data-stream in asnipe, which randomly swaps records of individuals and is considered best practice instead of node-based permutations because it maintains original data structure and controls for sampling bias (Farine, 2013, 2014, 2017; Farine and Whitehead, 2015). Significance was calculated by dividing the number of times the test statistic of the real network was smaller than the test statistics of randomised networks by 1000 (the number of permutations). All *P*-values generated using random networks comparisons are specified here as $P_{rand}$. Visualisations of networks were constructed in Gephi (version 0.9.2) (Bastian, Heymann and Jacomy, 2009) with a force-atlas layout that clustered together more strongly associating nodes.

We tested if hihi formed non-random associations in their groups compared to permuted networks using the coefficient of variation ("cv"). The value of cv describes variation in edge weights across a network: extreme values of cv are 0 and 10, but any values over 0.6 are considered to represent differentiated networks (groups are comprised of strong, repeated connections) (Farine and Whitehead 2015). We then explored if non-random associations were explained by strengths of bonds between individuals depending on their age class (adult and juvenile "assortment"). We tested for assortment in edge weights using the assortnet package (version 0.12) (Farine, 2014) to generate an assortment coefficient (*r*, a value from -1 to 1) which we compared to the *r* values of permuted networks. Positive assortment suggests similarly characterised individuals form stronger associations, while negative assortment indicates disassociation (Newman, 2002; Farine, 2014). Following evidence of different levels of associations between the different age groups, we considered if site use patterns uncovered during multistate analysis explained associations between juveniles. In a juvenile-only network we confirmed non-random associations across groups, because of evidence for differential site usage by individuals from our initial multistate analysis which could have structured associations across sites (Farine, 2017). We also investigated associations within groups to assess if juveniles had non-random associations on a finer scale. We compared the cv values of our network to cv values from permuted networks with data swapped across groups and then within groups. Finally, we explored assortment in association strengths depending on the primary group each juvenile was most commonly recorded in across all surveys, by comparing to the assortment coefficients of permuted networks.

**Behavioural interactions**

To explore how adult and juvenile hihi behaved in groups, for each individual we calculated the proportion of its observations where it was recorded interacting with another bird (separate observations were more than thirty seconds apart) and compared proportions between ages with a Wilcoxon rank sum test. Using proportions accounted for differences in survey effort so that we could combine data from all years. For each juvenile, we then calculated the proportion of total interactions allocated to each behaviour in Table 3.2 and explored if particular types of interactions were correlated using a Principle Components Analysis (PCA) (Budaev, 2010). For any principle components that explained 75% of variance, we next assessed how they correlated with network associations and whether juveniles that behaved in particular ways were more central in the network. We extracted weighted degree scores from our network for each juvenile each year, which explained the number and strength of associations for each bird and thus its placement in the network (animals with more connections tend to be placed more centrally (Krause *et al.*, 2015)). We ranked degrees and divided ranks by the number of juveniles each year, to calculate a proportion rank that was comparable across the different years of the study. We then constructed a GLM with each juvenile's degree rank as the response and any identified principle components as predictors. To account for non-independence in network data, we generated *P*-values by comparing our observed coefficient to coefficients generated from 1000 models where degree rank values were calculated from permuted networks (Farine and Whitehead, 2015).

## *Results*

There were two groups in 2015 and three groups for each of 2016 and 2017, in gully areas (away from feeders) containing water sources and mixed forest. Each year, hihi had multiple associates (mean ± S.E. number of associates: juveniles: 2015 = 15.71 ± 1.59; 2016 = 24.01 ± 1.63; 2017 = 25.29 ± 1.84; adults: 2015 = 8.21 ± 1.00; 2016 = 8.57 ± 1.23; 2017 = 9.84 ± 1.00). The 2015 network represented 379 associations between 33 adults and 31 juveniles; 2016, 1168 associations between 54 adults and 78 juveniles; and 2017, 1400 associations between 61 adults and 87 juveniles. The "gmmevents" event lengths defining associations corresponded to the length of time hihi were re-sighted across consecutive time blocks (median length of event windows (seconds): 2015 = 119.79, 2016 = 90.44, 2017 = 90.75; median re-sighting periods (seconds): 2015 = 90, 2016 = 90, 2017 = 120; Wilcoxon rank sum test comparing length of event windows to re-sighting periods, 2015: $W$ = 123240, $P$ = 0.06, 2016: $W$ = 541210, $P$ = 0.54; 2017: $W$ = 824380, $P$ = 0.17). Both the juvenile/adult and juvenile-only networks showed non-random (preferred and avoided) associations each year (juvenile/adult network: 2015: cv = 2.64, $P_{rand}$ = 0.03; 2016: cv = 3.60, $P_{rand}$ < 0.001; 2017: cv = 3.56, $P_{rand}$ = 0.008; juvenile-only network: 2015: cv = 1.77; 2016: cv = 2.31; 2017: cv = 2.46; in all years, $P_{rand}$ values across-location and within-location < 0.001).

**WERE JUVENILES MORE RESIDENT IN GROUPS THAN ADULTS?**

There was no difference in the numbers of adults and juveniles detected within and across years (Fisher's exact test: *N* juveniles = 207; *N* adults = 175; *P* = 0.18). However, juveniles were present on more days than adults (Wilcoxon rank sum test comparing number of days adults and juveniles were re-sighted: 2015: *W* = 235.5, *P* < 0.001; 2015: *W* = 235.5, *P* < 0.001; 2015: *W* = 235.5, *P* < 0.001). Consequently, our multistate analysis estimated that juveniles were re-sighted at least twice as frequently in successive survey occasions compared to adults in all three years (top-ranked models explaining re-sighting included age; Table 3.3; Figure 3.2a, b, c; Supplementary Table 3.1; juveniles *N*: 2015 = 37; 2016 = 79; 2017 = 91; adults *N*: 2015 = 45; 2016 = 62; 2017 = 68). Re-sighting was constant in 2015 and 2017 but varied across survey occasions in 2016 for both adults and juveniles (Supplementary Table 3.1) suggesting there were small variations in social behavior across years.

Networks reflected these general patterns in residency and showed strong positive assortment by age: each year at least 38% of associations occurred between juveniles only (Table 3.4; 2015: $r = 0.15$, $P_{rand} < 0.001$; 2016: $r = 0.25$, $P_{rand} = 0.028$; 2017: $r = 0.19$, $P_{rand} = 0.001$). Juveniles were also more likely to interact with others compared to adult hihi (Wilcoxon rank sum test: *W* = 8554.5, *P* < 0.001; although 67/207 juveniles were never observed interacting). Principle Component 1 (PC1) was strongly negatively loaded to "playfight" (Table 3.5; Supplementary Figure 3.1), which was the most frequent interaction (mean ± S.E. proportion of total interactions per juvenile that were playfights = 0.25 ± 0.02). Most remaining variation was represented by PC2 and PC3 (Table 3.5; Supplementary Figure 3.1). PC2 was loaded most strongly by "huddle" and "chased", but in opposite directions; this quantified variation in potential affiliative behaviours, because positive scores indicated individuals that huddled more were chased less often. PC3, on the other hand, was loaded negatively by "huddle" and "chased", but positively by "chase". This third component described variation where individuals that huddled less chased others more. For individuals that interacted, these three behavioural components did not significantly predict variation in network position (Table 3.6). However, there was a non-significant tendency that individuals with a more positive PC3 score (more likely to chase, less likely to be chased or huddle) had higher degree ranks (Table 3.6) suggesting that more dominant individuals may have tended towards being more social.

**Table 3.3.** Model-averaged estimates of re-sighting ($\rho$) and movement ($\Psi$) for adult and juvenile hihi in (a) 2015; (b) 2016 and (c) 2017. Estimates generated from multistate models in Supplementary Table 3.1 which had ΔQAIC weight > 0.00; significant estimates where confidence intervals (LCI, UCI) did not span 0.00 are highlighted in bold. Letters for movement correspond to group sites in Figure 3.2d, e, f.

(a)

| | Est. | LCI | UCI |
|---|---|---|---|
| **$\rho$ Adult** | **0.23** | **0.12** | **0.41** |
| **$\rho$ Juvenile** | **0.59** | **0.42** | **0.73** |
| $\Psi$ a to b Adult | 0.01 | 0.00 | 0.02 |
| **$\Psi$ a to b Juvenile** | **0.09** | **0.01** | **0.47** |
| $\Psi$ b to a Adult | 0.00 | -0.01 | 0.02 |
| $\Psi$ b to a Juvenile | 0.02 | 0.00 | 0.15 |

(b)

| | Est. | LCI | UCI |
|---|---|---|---|
| **$\rho$ Adult** | **0.17** | **0.09** | **0.31** |
| **$\rho$ Juvenile** | **0.36** | **0.22** | **0.53** |
| $\Psi$ b to c Adult | 0.00 | 0.00 | 0.00 |
| $\Psi$ b to c Juvenile | 0.00 | -0.02 | 0.02 |
| **$\Psi$ b to d Adult** | **0.04** | **0.01** | **0.23** |
| **$\Psi$ b to d Juvenile** | **0.15** | **0.09** | **0.31** |
| $\Psi$ c to b Adult | 0.00 | -0.01 | 0.02 |
| $\Psi$ c to b Juvenile | 0.02 | 0.00 | 0.11 |
| $\Psi$ c to d Adult | 0.02 | 0.00 | 0.11 |
| **$\Psi$ c to d Juvenile** | **0.09** | **0.04** | **0.19** |
| $\Psi$ d to c Adult | 0.01 | 0.00 | 0.07 |
| **$\Psi$ d to c Juvenile** | **0.04** | **0.02** | **0.10** |
| $\Psi$ d to b Adult | 0.01 | -0.01 | 0.03 |
| **$\Psi$ d to b Juvenile** | **0.04** | **0.01** | **0.23** |

(c)

| | Est. | LCI | UCI |
|---|---|---|---|
| **$\rho$ Adult** | **0.22** | **0.17** | **0.28** |
| **$\rho$ Juvenile** | **0.44** | **0.40** | **0.49** |
| $\Psi$ b to d Adult | 0.01 | 0.00 | 0.02 |
| **$\Psi$ b to d Juvenile** | **0.05** | **0.03** | **0.11** |
| $\Psi$ b to e Adult | 0.00 | 0.00 | 0.01 |
| $\Psi$ b to e Juvenile | 0.01 | 0.00 | 0.09 |
| $\Psi$ d to b Adult | 0.00 | 0.00 | 0.01 |
| **$\Psi$ d to b Juvenile** | **0.02** | **0.01** | **0.04** |
| $\Psi$ d to e Adult | 0.01 | 0.00 | 0.02 |
| **$\Psi$ d to e Juvenile** | **0.04** | **0.02** | **0.08** |
| $\Psi$ e to b Adult | 0.00 | 0.00 | 0.01 |
| $\Psi$ e to b Juvenile | 0.01 | 0.00 | 0.02 |
| **$\Psi$ e to d Adult** | **0.04** | **0.01** | **0.13** |
| **$\Psi$ e to d Juvenile** | **0.20** | **0.11** | **0.33** |

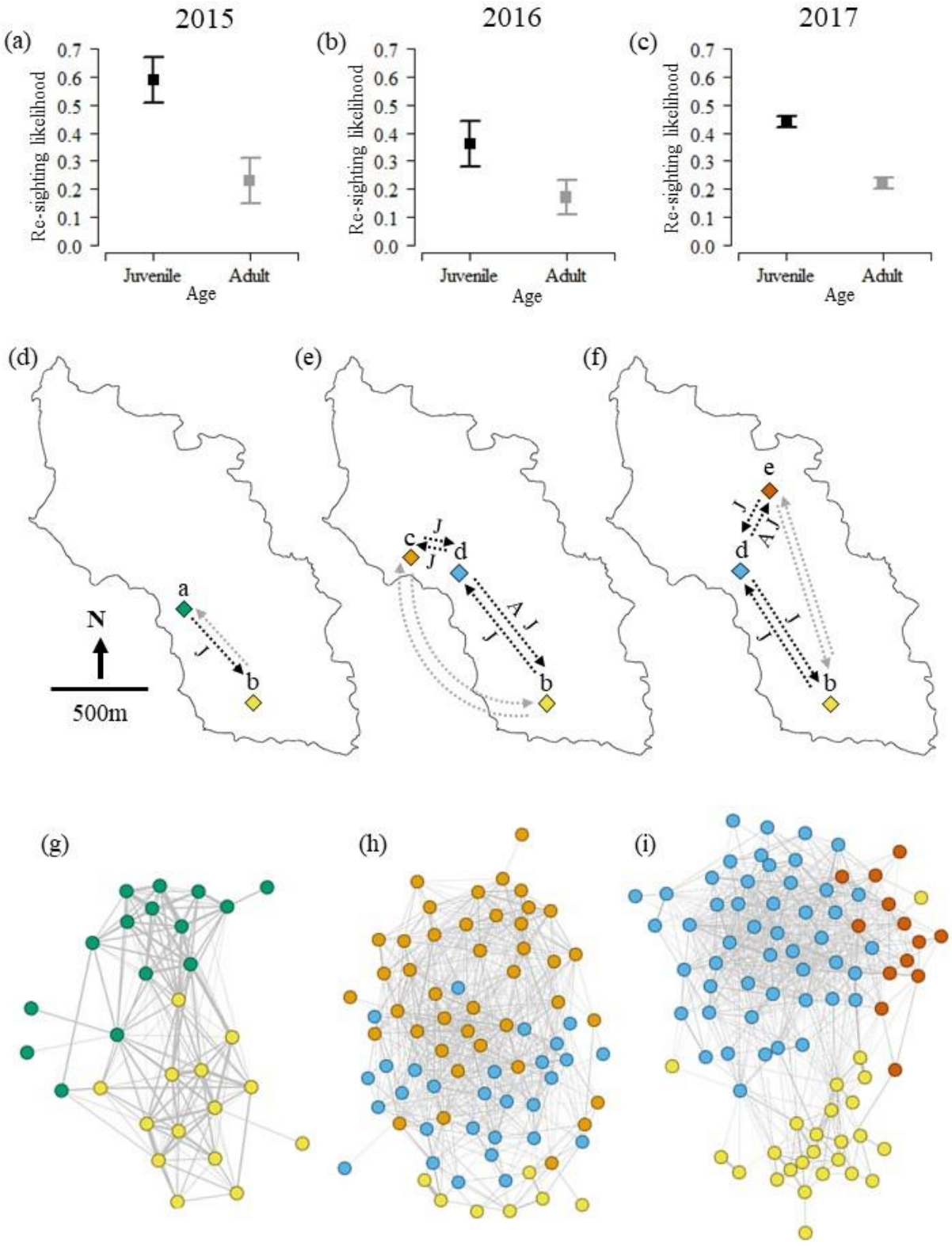



**Figure 3.2.** Re-sighting (a-c), movement (d-f) and associations (g-i) for groups (left = 2015; middle = 2016; right = 2017); (a-c) represent mean (± S.E.) re-sighting estimates for juveniles (black lines) and adults (grey lines); (d-f) show movements (dashed lines with arrowheads) between different groups for juveniles ("J") and adults ("A") (significant movements from Table 3.3 are black and lettered, non-significant movements coloured grey); (g-i) show social network diagrams where nodes (circles) represent each hihi and are coloured according to the location in (d-f) where they were seen most often. Lines (edges) represent associations. Strongly associating nodes cluster together more.

**Table 3.4.** Mixing matrices showing distribution of edge weights between adults ("A") and juvenile ("J") hihi for (a) 2015, (b) 2016 and (c) 2017 networks. $a_i^w$ are row sums, $b_i^w$ are column sums; due to rounding, sum values may not be exact. Tables are symmetrical so half the values are presented.

(a)

| | **A** | **J** | **$a_i^w$** |
|---|---|---|---|
| **A** | 0.208 | - | 0.414 |
| **J** | 0.206 | 0.381 | 0.587 |
| **$b_i^w$** | 0.414 | 0.587 | 1.000 |

(b)

| | **A** | **J** | **$a_i^w$** |
|---|---|---|---|
| **A** | 0.121 | - | 0.268 |
| **J** | 0.146 | 0.586 | 0.733 |
| **$b_i^w$** | 0.268 | 0.733 | 1.000 |

(c)

| | **A** | **J** | **$a_i^w$** |
|---|---|---|---|
| **A** | 0.111 | - | 0.273 |
| **J** | 0.162 | 0.565 | 0.727 |
| **$b_i^w$** | 0.273 | 0.727 | 1.000 |

**Table 3.5.** Principle components analysis (PCA) of juvenile social behaviours seen in group sites. The first three components accounted for more than 75% of variance (components 4-6 accounted for 21.5% variance in total and are not presented). Behaviours that loaded most on each PC are highlighted in bold.

| | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Chased | 0.13 | **0.62** | **-0.74** |
| Followed | 0.03 | 0.00 | 0.00 |
| Chase | 0.04 | 0.09 | **0.37** |
| Follow | 0.04 | 0.01 | 0.03 |
| Huddle | 0.16 | **-0.78** | **-0.54** |
| Playfight | **-0.98** | -0.03 | -0.17 |
| | | | |
| Eigenvalue | 0.11 | 0.07 | 0.06 |
| % variance explained | 36.7 | 23.2 | 18.6 |

**Table 3.6.** Results of a binomial GLM analysing variation in degree rank depending on PC1, PC2, and PC3 describing variation in interactions between juvenile hihi (Table 3.5). Coefficients, standard errors and *z* values are presented. Both the *P*-value of the model and the *P*-value generated using coefficients from 1000 randomised networks (specified as $P_{rand}$) are presented, for comparison. Marginal significance of PC3 indicated with "**.**".

| | | **coeff.** | **S.E.** | ***z*-value** | ***P*-value** | **$P_{rand}$** |
|---|---|---|---|---|---|---|
| degree ~ | intercept | 0.82 | 0.21 | 3.92 | < 0.001 | 1.00 |
| | PC1 | -0.53 | 0.55 | -0.97 | 0.33 | 0.87 |
| | PC2 | 0.33 | 0.57 | 0.57 | 0.57 | 0.49 |
| | PC3 | 0.56 | 0.81 | 0.68 | 0.50 | 0.06 **.** |

**DID GROUPS FORM IN STABLE LOCATIONS, OR DID THEY MOVE?**

Quantifying movement ($\Psi$) in our multistate analysis showed a low likelihood that hihi transitioned between group sites, although this did vary depending on where birds were moving to and from (Table 3.3, Figure 3.2d, e, f; Supplementary Table 3.1). Movement also depended on age, and some juveniles did move groups between each survey (Table 3.3; Figure 3.2d, e, f; Supplementary Table 3.1). However, on average only two or three juveniles moved between each survey (mean: 2015 = 2; 2016 = 3; 2017 = 3), and movement also varied among individuals (maximum number of moves per individual: 2015 = 3; 2016 = 7; 2017 = 7; juveniles that never moved groups: 2015 = 29/37; 2016 = 35/79; 2017 = 56/91). Furthermore, in the social network analysis we found that juvenile-only networks showed strong positive assortment by primary group in all three years, while associations among juveniles resident in different sites were much weaker (Table 3.7; Figure 3.2g, h, i; 2015: $r = 0.513$, $P_{rand} < 0.001$; 2016: $r = 0.32$, $P_{rand} < 0.001$; 2017: $r = 0.58$, $P_{rand} < 0.001$).

**Table 3.7.** Mixing matrices showing distribution of edge weights between juveniles depending on the group where they were most commonly located (site lettering refers to group locations in Figure 6) in (a) 2015, (b) 2016 and (c) 2017. $a_i^w$ are the row sums, $b_i^w$ are the column sums; due to rounding, sum values may not be exact. Tables are symmetrical so half the values are presented.

(a)

| | **Site a** | **Site b** | **$a_i^w$** |
|---|---|---|---|
| **Site a** | 0.330 | - | 0.450 |
| **Site b** | 0.121 | 0.429 | 0.550 |
| **$b_i^w$** | 0.450 | 0.550 | 1.000 |

(b)

| | **Site c** | **Site d** | **Site b** | **$a_i^w$** |
|---|---|---|---|---|
| **Site c** | 0.503 | - | - | 0.653 |
| **Site d** | 0.141 | 0.144 | - | 0.298 |
| **Site b** | 0.009 | 0.013 | 0.027 | 0.049 |
| **$b_i^w$** | 0.653 | 0.298 | 0.049 | 1.000 |

**(c)**

| | **Site d** | **Site b** | **Site e** | **$a_i^w$** |
|---|---|---|---|---|
| **Site d** | 0.575 | - | - | 0.674 |
| **Site b** | 0.028 | 0.155 | - | 0.189 |
| **Site e** | 0.071 | 0.006 | 0.061 | 0.137 |
| **$b_i^w$** | 0.674 | 0.189 | 0.137 | 1.000 |

**WERE JUVENILES RELATED TO ADULTS AND OTHER JUVENILES?**

In the re-sighting data each year there were very few occasions when juveniles were seen in the same group during the same survey as their parents (mean ± S.E. proportion of surveys: 2015 = 0.02 ± 0.02; 2016 = 0.03 ± 0.01; 2017 = 0.08 ± 0.02), or their maternal-siblings (Figure 3.3a; mean ± S.E. proportion of surveys: 2015 = 0.22 ± 0.08; 2016 = 0.25 ± 0.04; 2017 = 0.28 ± 0.04). Individuals that grouped closer to their nest-of-origin were not more likely to be seen with maternal-siblings each year (Figure 3.3b; null model highest ranked; Supplementary Table 3.2). Being recorded in more surveys also did not affect co-occurrence with maternal-siblings in any year (Supplementary Table 3.2). Together, this low likelihood of juveniles being resident with parents or maternal-siblings suggested that these individuals had very limited opportunities to associate, so we did not analyse assortment by relatedness in networks.

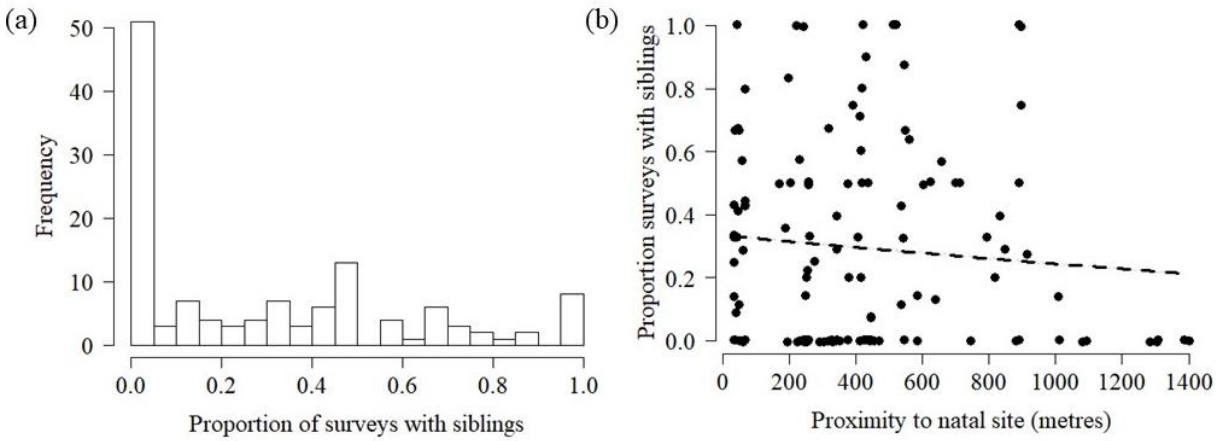



**Figure 3.3.** (a) Variation among juveniles in the proportion of occasions where they were recorded with their maternal-siblings (all years of the study included), and (b) relationship between proportion of occasions seen with siblings and the distance from each juvenile's natal site to where they grouped. In (b), confidence intervals were too narrow to plot (Supplementary Table 3.2).

## *Discussion*

Here we used both a multistate analysis and social network analysis approach to characterise the location use, age composition, and relatedness of hihi groups that form at the end of each breeding season. We found that groups formed non-randomly and occurred in consistent locations within each year, with little movement across our study site. Multistate analysis indicated that groups were formed predominantly of juveniles, and although some adults were observed their presence was more transient. Network associations reflected these differences in residency: rather than associating with adults, juveniles most strongly associated with other juveniles frequently present in the same group locations. Juveniles also interacted more frequently with other birds compared to adults. However, despite differences among individuals in the amount of affiliative- or aggressive-type interactions, the types of behavioural interactions did not significantly predict a juveniles' number of network associates. Finally, juveniles were almost never seen with their parents (occurred in only 2-8% of surveys across the study) and were also re-sighted without their nest mates in the majority (72-78%) of surveys. Together, these results suggest juvenile hihi groups most closely resemble the "gangs" described in juvenile ravens by Dall and Wright (2009) (Table 3.1), where juvenile birds aggregate around communal roosts (Wright, Stone and Brown, 2003) or other social meeting places (Ward and Zahavi, 2008) which are separate from main colonies and thus have limited interaction with adults. This is in contrast to flocks, which can move over large distances (Templeton *et al.*, 2012) or crèches, where juveniles associate with related adults (Balda and Balda, 1978).

Animals can aggregate if ecological factors (such as rich foraging grounds) cause them to coexist in the same place at the same time (Mourier, Vercelloni and Planes, 2012; Strandburg-Peshkin *et al.*, 2017; Gall and Manser, 2018), but location use can also arise as a consequence of preferring to associate with others (Fletcher, 2007; Firth and Sheldon, 2016). Similarly, while the diverse social structures that have evolved across the animal kingdom may influence interactions between phenotypically-different individuals, the inverse is also possible, where preference of associating with similar individuals leads to structured groups. Thus, the aggregations of juvenile hihi we detected here could have been a by-product of differential habitat use according to age to avoid competition with more dominant adults (Catterall, Kikkawa and Gray, 1989; Marchetti and Price, 1989; Sol *et al.*, 1998). Alternatively, groups could have arisen through juveniles choosing to associate with individuals of a similar phenotype (Croft *et al.*, 2005). Understanding the intricate link between current environment, group social structure, and how or why associations form is still a fledgling topic in social network analysis (Madden *et al.*, 2009; Godfrey, Sih and Bull, 2013; Pinter-Wollman *et al.*, 2013; Leu *et al.*, 2016). We did not explicitly test this link in this Chapter (for example, by changing the environment and comparing network structures (Formica *et al.*, 2016)) so cannot fully conclude if ecology or individual choice determined group associations. However, repeating observations across years did show similar characteristics in groups and their locations, albeit with a small level of variation, perhaps suggesting climatic conditions or other ecological variables of the sites affected group formation (Krause and Ruxton, 2002). Thus, the value of long term studies is that they allow for replicates that demonstrate whether the same determinants structure animal groups across years (Shizuka *et al.*, 2014) especially when individual identities differ year-on-year (as in our study, with different juvenile cohorts).

Regardless of whether groups arose due to active choice by individuals or a more incidental aggregation based on environment, the resulting non-random associations formed between juveniles could mediate behaviours such finding food, and avoiding predators or disease (Krause and Ruxton, 2002; Krause, Lusseau and James, 2009; Drewe, 2010; Aplin *et al.*, 2012; Schakner *et al.*, 2017). Associations from direct interactions (such as allogrooming) can transmit information between individuals: for example, animals can detect odours from other animals they contact (Galef and Laland, 2005). Direct contact is also important for other consequences of group living, as it can lead to the spread of disease (Hamede *et al.*, 2009). While aggregating, we observed juvenile hihi interacting directly with other individuals. Some behaviours (such as chasing, or being chased) could be establishing dominance in these groups (Drews, 1993). However, we also observed behaviours that were consistent with definitions of social play (*sensu* Bekoff and Allen, 1998; Diamond and Bond, 2003). Social play is known in other gang-forming juveniles (ravens) (Heinrich and Smolker, 1998; Diamond and Bond, 2003) and is generally thought to be a more complex behaviour associated with large brain sizes, but previous reviews have cautioned that its apparent absence in other species could be due to a lack of research (Diamond and Bond, 2003). Further observation is needed to be confident that this was play behaviour in hihi, and so we use the term “playfight” cautiously here, but such interactions between juveniles have been suggested to be one route by which information is shared in other species (Diamond and Bond, 2003). However, we did not find a significant link between likelihood of interacting and network position

(degree). As an individual's number of associates can be important for information acquisition (Aplin *et al.*, 2012; Snijders *et al.*, 2014), this may indicate interactions and familiarity between specific individuals are not crucial to information dissemination in young hihi (Schwab, Bugnyar and Kotrschal, 2008; Guillette, Scott and Healy, 2016; Ramakers *et al.*, 2016), Instead, local enhancement or observing individuals co-occuring in the same place at the same time may provide information about the current environment (Aplin *et al.*, 2012). As yet, it remains unclear what structures juvenile hihi network position in groups, so further work is needed to test why groups form and how this influences sociality, to help further understand the importance of group structure for learning in young birds.

As we found limited co-occurrence and associations between differently-aged animals, are there benefits to aggregating with other juveniles rather than adults? This could be a potentially risky strategy as young animals are naïve (Galef and Laland, 2005) and do not always behave appropriately to suit the current environment (Clayton, 1994). Individuals appear to recognise these risks in some species (such as capuchin monkeys, *Cebus apella*) and prefer to pay attention to adults rather than juveniles if given the choice (Ottoni, De Resende and Izar, 2005). However, in gang-type groups the limited presence of adults creates little opportunity to associate with these more experienced individuals, in contrast to flocks (Templeton *et al.*, 2012) or crèches (Heinsohn, 1991). While young animals by themselves may be naïve, large groups of juveniles are still thought to be beneficial because they can act as "information centres" (Dall and Wright, 2009) where associating with many animals collectively gathering and sharing information may help overcome any one individual's inexperience (Ward and Zahavi, 2008). For example, in quelea (*Quelea quelea*), parents leave their young after approximately three weeks of care, and young then form assemblages which help them to exploit their habitat and forage successfully without learning from adults (Ward and Zahavi, 2008). Similarly, juvenile raven gangs respond collectively to new, ephemeral, food sources (Marzluff, Heinrich and Marzluff, 1996; Dall and Wright, 2009). Furthermore, in this context other factors such as relatedness may not be important for grouping because non-kin provide a broader range of information collected from different experiences, which could be more relevant to the current environment (Schwab, Bugnyar and Kotrschal, 2008; Kulahci *et al.*, 2016). Young animals are known to pay more attention to non-kin particularly when early life conditions were suboptimal, suggesting they adjust associations depending on payoff (Farine, Spencer and Boogert, 2015). Hihi do have high rates of extra-pair paternity (Brekke *et al.*, 2013), and unfortunately genetic data was not available at the time of the study, but the general low presence of adults or half-siblings suggests relatedness was not important to their grouping (Saitou, 1978, 1979; Hirsch *et al.*, 2013; Arnberg *et al.*, 2015). Overall, if hihi juvenile groups may be information centres then it will be valuable to test how they inform foraging behaviour.

To conclude, we show that juvenile hihi are commonly found in groups during their first few months of independence from parents. These groups form in spatially-separated locations and are dominated by juveniles, with little opportunity to interact with adults. The structure of gang-like groups in young hihi create the potential for many naïve individuals to associate, and potentially share information, Next, it

will be valuable to test more explicitly whether these groups inform behaviour in young hihi. By doing so, we can explore if such groups provide opportunities to help young birds overcome any one individual's disadvantage of being naïve, or whether there are downsides of associating with inexperienced peers.

# CHAPTER 4

# Copy parents or follow friends? Juvenile foraging behaviour changes with social environment

*I gratefully acknowledge Mhairi McCready for PIT-tagging hihi for this Chapter*

The first few months of juvenile independence is a critical period for survival, as young must learn new behaviours to forage efficiently. Social learning by observing parents (vertical transmission) or others (horizontal/oblique transmission) may be important to overcome naivety, but these tutors are likely to differ in their reliability due to variation in their own experience. How young animals use different social information sources, however, has received little attention. Here we tested if wild juvenile hihi (*Notiomystis cincta*, a New Zealand passerine) retained foraging behaviours learned from parents, or if behaviour changed after independence in response to peers. We first trained parents with feeders during chick rearing: one-third could access food from any direction, one-third could access food from one side only, and the remaining third had no feeder. During post-fledge parental care, juveniles chose the same side as their parents. Once independent, juveniles formed mixed-treatment groups naturally so we then presented feeders with two equally profitable sides. Juveniles with natal feeder experience were quicker to use these feeders initially, but side choice was now random. Over time, however, juveniles converged on using one side of the feeder (which differed between groups). This apparent conformity was because juvenile hihi paid attention to the behaviour of their group and were more likely to choose the locally-favoured side as the number of visits to that side increased. They did not copy the choice of specific individuals, even when they were more social or more familiar with the preceding bird. Our study shows that early social experiences with parents affect foraging decisions, but later social environments lead juveniles to modify their behaviour.

## Introduction

The first few months of independent life are a critical period for survival in many bird species. Studies have reported that only 50% of young survive the first two months after leaving parents (Cox *et al.*, 2014; Naef-Daenzer and Grüebler, 2016), and in some populations first-year survival can be as low as 11% (Sullivan, 1989; 30% first-year survival reported by McKim-Louder *et al.*, 2013). Mortality rates often peak over winter and can reach five times that of adults as juveniles struggle to survive in harsh environmental conditions (Goss-Custard and Durell, 1987; Daunt *et al.*, 2007). What determines individual survival is likely to be non-random (Naef-Daenzer and Grüebler, 2016), and starvation plays a key role (Ringsby, Sæther and Solberg, 1998; Sol *et al.*, 1998; Daunt *et al.*, 2007; Low and Pärt, 2009). However, little is known about how young birds learn to find food and survive during their first few months (Cox *et al.*, 2014).

One general problem for young animals is their inexperience compared to adults (Galef and Laland, 2005). This means they have had limited opportunities to learn to find, capture, and process food (Marchetti and Price, 1989; Wheelwright and Templeton, 2003), which can limit their foraging efficiency. For example, juvenile garter snakes (*Thamnophis atratus hydrophilus*) feed on a more restricted range of food types than adults (Lind and Welsh, 1994), and studies in young birds show they take longer to forage than adults (Daunt et al., 2007; Gochfeld and Burger, 1984; Kendal et al., 2009; Marchetti and Price, 1989; Sol et al., 1998). Therefore, juveniles need to learn new behaviours to improve their efficiency. However, learning also presents a challenge to juveniles and they may take longer than adults to acquire new skills (Franks and Thorogood, 2018). If young animals face both a greater need to learn and an increased cost of learning, are there strategies they can use to overcome these combined challenges? Paying attention to the behaviour of others can be one way for juveniles to buffer their own inexperience (Galef and Laland, 2005; Kendal *et al.*, 2005; Kitowski, 2009; Clutton-Brock, 2016; Griesser *et al.*, 2017) and young animals encounter a variety of sources of social information during their first few months.

Before they become fully independent, naïve juveniles can learn important behaviours from their parents ("vertical transmission" (van Schaik, 2010)), such as preference for or aversion to certain foods (Galef and Giraldeau, 2001), or foraging techniques (Rapaport, 2006; Geipel *et al.*, 2013). In some cases, experiences with parents have long-term effects on behaviour later in life. For example, cross-fostered blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) shifted their foraging niche in the direction of their foster parents and maintained this preference to adulthood when feeding their own young (Slagsvold and Wiebe, 2011). Reliable vertical social learning is in the best interests of both parents and juveniles, because it increases offspring survival and maximises lifetime reproductive fitness (Clutton-Brock, 1991; Laland and Kendal, 2003; Thornton and Clutton-Brock, 2011). However, if parental

information is less optimal (Farine, Spencer and Boogert, 2015) or environments change so that behaviours learned in early life become outdated (Wong and Candolin, 2014), then young animals should pay attention to other information to update behaviour.

Once independent, juveniles encounter other individuals ("peers"). When peers are present in the same location, at the same time, and encounter the same environment as the naïve individual, learning via other juveniles (horizontal transmission") and adults ("oblique transmission") (van Schaik, 2010) may provide more up-to-date information. Under some conditions, animals rely on copying the behaviour of peers to such an extent that one behaviour becomes predominant in a group, leading to conformity across individuals (van de Waal, Borgeaud and Whiten, 2013; Aplin *et al.*, 2015b). However, peer-provided information could conflict with previous information from parents and can also be unreliable for a variety of reasons. Peers may provide deliberately misleading information: for example, fork-tailed drongo (*Dicrurus adsimilis*) use false alarm calls to scare others away from food (Flower, 2011; Flower, Gribble and Ridley, 2014). Peers can also learn incorrectly, so juveniles risk copying maladaptive behaviours (Curio, Ernst and Vieth, 1978; Laland and Williams, 1998; Franz and Matthews, 2010). Finally, animals have preferred and avoided companions, forming "social networks" which determines what peers and social learning opportunities they encounter (Krause, Lusseau and James, 2009; Kurvers *et al.*, 2014; Krause *et al.*, 2015). Variation in familiarity can influence social information use, although sometimes animals may prefer to learn from familiar partners (Swaney *et al.*, 2001; Guillette, Scott and Healy, 2016), while others use unfamiliar sources which have different personal experiences (Ramakers *et al.*, 2016). Further, individuals that interact with many peers (have a high "degree") encounter many sources of information, and may acquire behaviour faster or gain a more complete picture of the environment (Aplin *et al.*, 2012; Tóth *et al.*, 2017).

Both theory and empirical studies have discussed how animals adjust their use of social and personal information to best suit current conditions (Kendal, Coolen and Laland, 2004; Kendal *et al.*, 2005; Thorogood and Davies, 2016), but less is known about how they trade off or integrate different sources of social information from parents and peers (Laland, 2004; Farine, Spencer and Boogert, 2015). This may be important for understanding how behaviours learned early in life persist, particularly in social groups where animals do not associate randomly. Hihi (*Notiomystis cincta*), a threatened New Zealand passerine, provide an ideal opportunity to investigate social information use in young wild birds. In one population (Tiritiri Matangi Island), hihi nest and raise their altricial chicks in monitored nest-boxes in territories during the breeding season (September-February). Fledglings are cared for by parents for two weeks before dispersing from the nest site, and then form groups of independent juveniles in reliable locations on the island (Chapter 3). The time with parents and in groups likely provides opportunities for social learning, but how these different sources of information are used has not been investigated. Finally, understanding the importance of social learning for foraging in young hihi may help us understand how they adjust feeding behaviour following conservation interventions, particularly when provisioning supplementary food is a crucial part of conservation management for hihi (Cox *et al.*, 2014).

To test the hypothesis that social experiences in early life affect foraging behaviour of juvenile hihi, we set up novel feeders at nests and at sites where groups congregate. We predicted (1) young hihi use social information provided by parents during their first couple of weeks post-fledging; and (2) this information continues to influence their behaviour once independent. However, if (3) juveniles pay more attention to social information in groups, then their behaviour would change once independent and depend on social characteristics (tie strengths and degree). Finally, to highlight how the inexperience of juveniles changes their learning strategies we also predicted (4) juvenile hihi respond to social information more than adults. By recording sequential visits to feeders, we could detect copying and changes in behaviour through time.

## *Methods*

### STUDY POPULATION

We conducted our experiment during one breeding season (October 2015 – April 2016) on Tiritiri Matangi Island (36°36'00.7"S, 174°53'21.7"E). The study population of hihi numbered c. 88 adults and 132 juveniles (juveniles: any fledgling from the 2015-2016 breeding season, adults: all other birds) (McCready and Ewen, 2016). Each individual was identifiable from a unique combination of coloured leg rings. During our study hihi also carried a Radio Frequency Identification (RFID) Passive Integrated Transponder (PIT) tag (from here, "PIT tags") integrated into one of the leg rings (IB Technology). This enabled remote recording of visits to feeding stations fitted with antenna and data-loggers (IB Technology model EM4102).

### (1) LEARNING WITH PARENTS AT NESTS

#### Experimental procedure

We divided active nests into three treatment groups (Figure 4.1a): "no feeder" (naïve); an "open feeder" which could be entered from any direction so hihi learned to recognise feeders as a food source; and a "side-choice feeder", where only one of two channels (left, LHS or right, RHS, assigned equally among nests) contained a sugar water reward so hihi learned an association and a side choice. These feeder treatments ensured that fledglings had different experiences of feeders with parents. Nests were allocated based on their location and surrounding forest maturity, which balanced rearing conditions of chicks and avoided movement between different treatments. Each treatment contained similar numbers of nests and fledglings (Figure 4.1a). We only included first clutch nests in treatments to avoid fledglings encountering different feeders at any later second-clutch nests once they dispersed from the nest site.

Between November 2015 and January 2016, we set up feeders 10 days after chicks hatched, approximately 10 metres from nest-boxes. This gave parents two weeks to learn to use the feeders before chicks fledged (hihi fledge 28 days after hatching). Sugar water was provided in semi-opaque brown bottles attached to Perky Pet® feeder bases (213 Pop Bottle Hummingbird Feeder) which did not provide hihi with visual information about contents prior to foraging. Feeders were checked daily; if we did not observe at least one parent using the feeder in the first three days, we moved it following protocols used in previous studies (Ewen *et al.*, 2008; Thorogood, Ewen and Kilner, 2011). At all side-choice feeders, parents first showed no preference for a side (exactly half of all first visits were to the rewarding side) but then learned to use the reward side before chicks fledged (Appendix 1.3). Parents did not use open feeders at 6 of the 15 nests, but as their fledglings (*N* = 13) still had an opportunity to observe the feeder in the parents' territory, we retained them in the treatment group for later analyses.

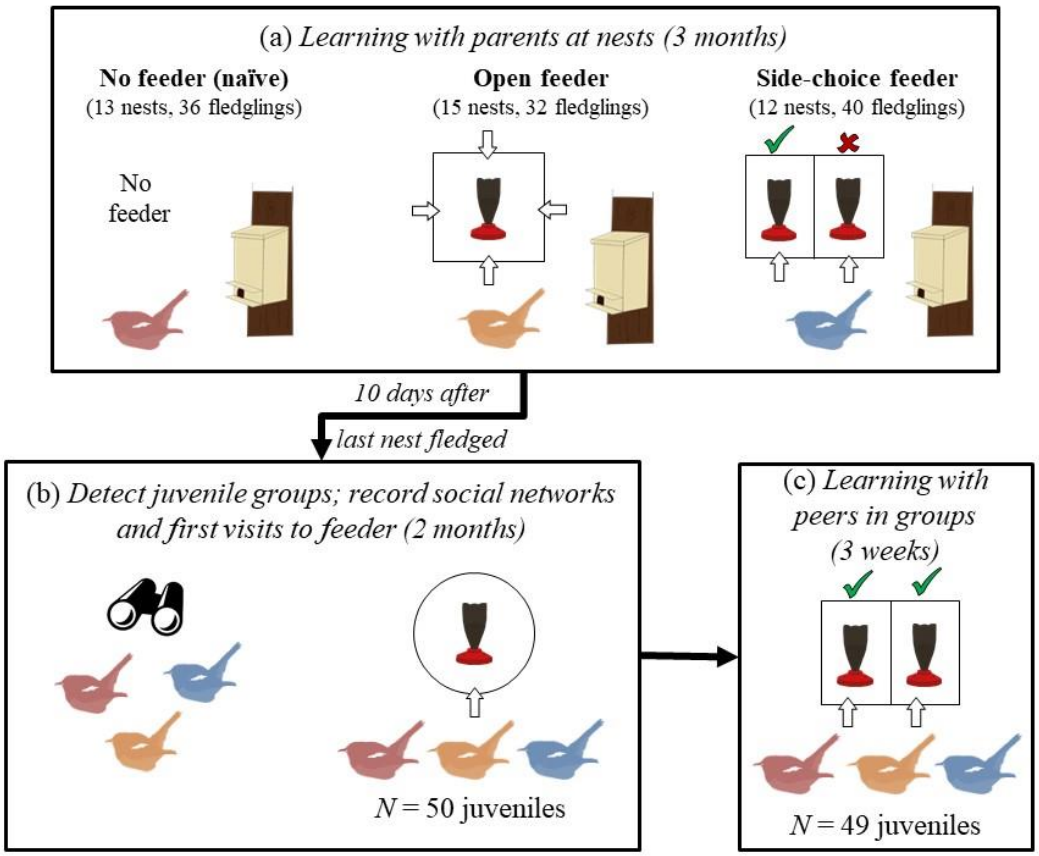



**Figure 4.1.** The stages of the experiment: (a) learning with parents at nests, showing feeder designs for each treatment, number of nests and fledglings assigned to each treatment group (no feeder: red, open feeder: orange, side-choice feeder: blue); (b) detecting juvenile group sites (containing a mixture of juveniles from each nest treatment group), then recording visits to a supplementary feeder to assess how quickly juveniles from different treatment groups visited feeders and construct a social network; (c) learning with peers at side-choice feeders once independent and in group sites. Not all juveniles were consistently present throughout all of (b) and (c).

After chicks fledged, we observed visits to all feeders (for 45 minutes each, at least every second day) and also recorded visits to side-choice feeders with RFID data-loggers at entry points. Additionally, we monitored feeder visits to side-choice feeders using Bushnell NatureView HD® trail cameras placed approximately 50cm from the feeder. We accounted for differences between continuous recording at side-choice feeders and the shorter observations at open feeders in later analyses by only considering if we ever recorded use by each fledgling, rather than the frequency or time of use. After each observation period, we located and identified any fledglings additionally heard within a c.15-metre radius of the feeder. We removed nest feeders once fledglings were not seen or heard at the nest site for two consecutive days (suggesting they had dispersed, or died); this occurred on average 10 days after fledging (range 0 – 13 days). At any nests where we never heard or saw fledglings, we waited 10 days before taking down feeders.

**Data analysis**

All analyses (of both parent and peer effects) were conducted in R (version 3.5.0) (R Core Team, 2017). We used a binomial sign test to determine if fledglings made the same choice as their parents when first visiting side choice feeders. We compared the number of instances when fledglings from side-choice feeder nests chose the same side (LHS or RHS) as their parents to an expected random chance of 0.5.

**(2) LEARNING WITH PEERS IN GROUPS**

**Detecting juvenile groups, and recording a social network**

We started surveying for juvenile groups 10 days after the last nest fledged. Every day for three weeks we recorded ring combinations of all hihi sighted during one-hour surveys conducted in six forested gullies across the island (Figure 4.1b). We selected two sites c. 300 metres apart ("Site 1" and "Site 2") where we consistently recorded the most juveniles (Chapter 3). These sites were located in latitudinally-orientated valley gullies containing mature remnant forest that were separated by a parallel ridge with open pasture. To record a social network (Figure 4.1b) before testing for retained responses from nests or for horizontal transmission from peers (Figure 4.1c), we set up a feeder with one entry point (i.e. no side choice) at each of these two group sites for six weeks. We recorded time-stamped visits with a RFID data-logger at the entry point and collected a total of 11928 visits by 50 juveniles (plus 14 adults that also visited). We used these visits to construct one weighted social network with the function "gmmevents*"* in the R package asnipe (Farine, 2013), which calculates associations based on similarities in timings of visits. Any juveniles that visited fewer than three times ($N = 3$) were excluded. Using this network, we calculated each individual's degree centrality (number of and strength of associations), and tie strengths between hihi (number of times each pair of hihi in the network associated). Most juveniles present in later stages of the experiment used these "network feeders" (42/50), so by the end of network data collection the majority of juveniles had experienced entering a

feeder, but not all had experience of a side-choice design (20/50 from side-choice feeder nests). The 8 juveniles that arrived after network recording did not have degree or tie measures during later analysis of effects of sociality on foraging behaviour. No new hihi were recorded after six weeks, suggesting that the majority of hihi using group sites were included in the network.

**Learning from peers**

Following network recording, we replaced network feeders with our side-choice feeder design; however, now both sides were equally rewarding and contained sugar water (Figure 4.1c; Figure 4.2). These feeders tested for retained side preference from nests, or effects of peers on foraging behaviour (side choice). During set-up, we ensured that the location and density of vegetation surrounding the feeder was as similar as possible to limit external influences on side choice. We recorded visits to both sides using an RFID data-logger at each entry point and also placed trail cameras 1 metre from feeders to record visits; these data were also used to cross-check PIT tag reliability (Appendix 2.2). We continued observations on alternate days in a 10-metre radius of the feeder (total of 25 one-hour observations per site) and recorded identities of hihi present in 30-second time blocks (120 blocks per survey). These observations were used to indicate how long hihi spent near the feeder when they could be observing others (but not necessarily visiting the feeders and detected by the RFID system; Appendix 2.2). Feeders were set up for three weeks (at Site 2, no visits were recorded for days 14 and 15 because of problems with the RFID data-loggers).

In total across (during surveys, network recording, and feeder presentations), we recorded 62 first-clutch juveniles (no feeder $N = 15$; open feeder $N = 22$; side-choice feeder $N = 25$), although not all individuals were observed during each stage of the experiment. There was no difference in the proportion of fledglings recorded from nests with or without feeders (Fisher's exact test of fledglings detected at group sites; from nests with feeders = 47/74; from nests without feeders = 15/29; $P = 0.37$). We also recorded 9 second-clutch juveniles. We added these individuals to the naïve treatment in later analyses as there was no evidence they appeared at group sites any later than naïve first-clutch juveniles (compared ranked order of arrival; Wilcoxon rank sum test: $W = 30$, $P = 0.12$).


**Figure 4.2.** Photos of feeder set-up for juvenile groups in (a) Site 1; (b) Site 2. "X" and "O" symbols were used for another experiment, but "X" is always left, "O" right. Photo credits: Rose Thorogood.

**Data analysis**

For analyses using Generalised Linear Models (GLMs) or Generalised Linear Mixed Effect Models (GLMMs), we used a model selection approach (Burnham and Anderson, 2002; Symonds and Moussalli, 2011; Harrison *et al.*, 2017) in the R package AICcmodavg (Mazerolle, 2017). We ranked candidate Generalised Linear Models (GLMs) or Generalised Linear Mixed Effect Models (GLMMs) that included all possible combinations of relevant predictors by their corrected Akaike Information Criterion (AICc). For all models within 2 AICc units of the top-ranked model, we calculated averaged effect sizes (±95% confidence intervals) of included predictors to assess their effect (Burnham and Anderson, 2002; Nakagawa and Cuthill, 2007). Any effect where confidence intervals did not span 0.00 were considered significant. GLMMs were implemented using the lme4 package (Bates *et al.*, 2015).

*First visits: did juveniles retain behaviour from experiences with parents?*

To detect any effects of nest experiences once juveniles were independent, we ranked the times of first visits (latency in seconds from the very first visit, specified as 0 seconds) for all juveniles that visited during feeder presentations ($N$ = 58: naïve = 21; open feeder = 16; side-choice feeder = 21), which accounted for non-normally distributed times. This included eight juveniles that only visited after the network feeder (naïve = 5, open feeder = 2, side-choice feeder = 1). We used Poisson-distributed GLMMs to analyse variation in arrival rank depending on whether a feeder was present or absent at nests, and for juveniles from nests provided with feeders, whether they or their parents had used feeders and the feeder type. We included a random intercept to account for whether juveniles arrived for the first time during network recording or experiment feeders.

We tested for a bias in side choice across all juvenile first visits using a Fisher's exact test to compare the number of LHS and RHS choices by all juveniles to a random distribution within and across sites. We also used a binomial sign test to test whether the subset of juveniles from side-choice nests retained a side preference by comparing the number of times individuals chose their nest reward side to a random choice (50% of visits). Finally, we assessed if first choice was socially-mediated using a binomial GLM to analyse if juveniles chose the same side as the preceding bird (yes = 1, no = 0) depending on how closely they followed that bird in time ($log_{10}$-transformed seconds between visits because times were not normally distributed).

*Ongoing visits: did juveniles copy peers?*

We investigated changes in side choice by groups over the course of the experiment (mean ± S.E. days individuals were recorded visiting feeders = 11.47 ± 0.80). We calculated the proportions of all visits made per day to the RHS at each feeder (including all visits irrespective of age) and used binomial GLMs to test if changes in daily group preference depended on experiment day and group site. Following the results from this initial analysis, we began investigating individual level patterns. To test if juveniles from side-choice nests continued to prefer their nest reward side, we calculated the proportions of visits each side-choice nest juvenile made per day to the RHS. We used GLMMs to investigate if this proportion changed across experiment days and depending on nest side (RHS or LHS) between the two group sites. Preference would differ between juveniles across days if side choice resulted from nest treatment, so we included an interaction between nest side and experiment day. Our random intercept was individual identity to account for repeated data-points for the same birds. To further explore that juveniles from opposite side-choice feeder nests were mixed between the two groups and did not drive changes in side preferences, we compared the proportion of each juvenile's total visits made in Site 1 between RHS and LHS side-choice nest juveniles, using a Wilcoxon rank sum test.

Juvenile groups contained a mix of birds from different nest treatments (Figure 4.1), so we analysed if hihi copied (i) the behaviour of the social group and (ii) the behaviour of specific individuals, on each visit. For (i), we analysed if hihi chose the side favoured by each group by the end of the experiment (the "locally-preferred side": Site 1 = RHS, Site 2 = LHS), depending on group preference. For each visit, we calculated the group's preference as the frequency of preceding visits made that day to the locally-preferred side. Although frequency of behaviour may not represent the preference of all individuals if some individuals visit more often (Aplin *et al.*, 2015a; van Leeuwen *et al.*, 2015, 2016; Whiten and van de Waal, 2016), we initially calculated frequency of behaviour and frequency of individuals and they were strongly correlated (Pearson correlation: $r = 0.81$, $P < 0.001$). Thus, we used frequency of behaviour as our measure of group preference, which does not require hihi to recognise and track individuals (Aplin *et al.*, 2015a, 2015b). Binomial GLMMs were then used to test if an individual's side choice at each visit matched the locally-preferred side (1), or did not match (0) depending on group preference, or if there were effects of day of experiment (days 1-21, to assess if side choice varied more

with social environment or personal learning (Aplin *et al.*, 2015a, 2015b)), time of day (hours; individuals visiting later in the day could have observed more visits), the focal bird's degree score from the network (as a measure of the effects of sociality on behaviour), and age (to test if juveniles used social information differently to adults).

To explore if (ii) hihi copied specific individuals, we calculated the proportion of times each individuals' side choices were matched by the bird that visited next. We then used binomial GLMMs to explore if individuals that visited closer in time to the preceding bird ($log_{10}$-transformed seconds to account for non-normally distributed times) were more likely to choose the same side (no = 0, yes = 1). Including time allowed us to explore if temporal proximity allowed for stronger copying, or conversely if closely-following individuals avoided each other to limit competition for resources (Krebs and Inman, 1992). We also included additional fixed effects of tie strength (familiarity) and focal individual degree (sociality) to investigate social effects on copying specific individuals, and age of both the preceding hihi and the focal individual (age could affect social information use). Finally, we included measures of group preference per visit, to assess how copying specific individuals affected side choice in addition to any effects from the broader social environment. As a random intercept, we included individual identity to account for repeated visits by individuals.

Most juveniles moved between group sites at least once (32/49 juveniles, but only two adults), so we repeated analyses for (i) and (ii) to test if limited or outdated personal information affected copying after changing sites in juveniles (Laland, 2004; Kendal *et al.*, 2005). Explanatory variables were the same as in the first sets of analyses (excluding age), but we also included number of site changes (because earlier experiences could affect side choice). For analysis of choice of locally-preferred side depending on the behaviour of the group, we additionally included the proportion of visits each juvenile made to the preferred side at the previous site on the previous day, as individuals with a stronger preference for a side may have been less likely to switch sides after moving.

## *Results*

### LEARNING WITH PARENTS AT NESTS

Only fledglings of parents that used feeders themselves (at 60% of open and 100% of side-choice feeders) were detected using feeders at nest sites (open: 7/32 fledglings at 4/15 nests; side-choice: 11/40 fledglings at 5/12 nests). At nests where parents did not use feeders some fledglings were not observed around the nest site after fledging (*N* = 6 nests, 13 fledglings), but this was not only due to mortality as 9/13 were recorded once they were independent. Where we did not observe any feeder use, we were confident hihi did not use feeders at other times as there was no sugar water taken or residue left behind on feeder bases (which we saw at feeders with confirmed use).

The majority of the 11 fledglings that visited side-choice nest feeders (5 nests) chose the same side as their parents on their first visit (9/11 used same side; Binomial sign test: *P* = 0.03). At all five nests, we observed fledglings follow a parent into the vicinity of the feeder while begging (Figure 4.3a, b), and then follow a parent into the feeder (often still begging) (Figure 4.3c). Five fledglings visited feeders only once; in the remaining six, their number of visits ranged from 3 – 51. Five out of six fledglings maintained a preference for their side but occasionally also visited the other side (mean = 74% preference).


**Figure 4.3.** Behaviour of fledglings with parents at side-choice feeders. (a) Two fledglings (left) follow mother (right) to feeder; (b) a fledgling (right) in begging posture, while parent is in feeder; (c) fledgling enters feeder following a parent (out of frame on right). “X” and “O” symbols were used for another experiment, but “X” was always left, “O” right. Images captured using trail cameras.

**LEARNING WITH PEERS IN GROUPS**

**First visits: did juveniles retain behaviour from experiences with parents?**

Juveniles from nests with feeders were quicker to use group site feeders than juveniles from nests with no feeder (*N* = 58; 9/10 of the first juveniles were from nests with feeders; effect of feeder presence on arrival rank = -0.27±0.05, 95% CI = -0.37 – -0.18; Figure 4.4; Supplementary Table 4.1a). However, the details of early life experiences were not important for juveniles from nests with open and side-choice feeders: models containing parents' use of the feeder, the type of feeder, and if a juvenile had used its nest-site feeder were ranked lower than the null model (Figure 4.4; Supplementary Table 4.1b). Furthermore, juveniles from side-choice feeders did not significantly prefer the side experienced at the nest (binomial sign test, 10/16 juveniles chose nest side on first visit, *P* = 0.46), even when they had used nest feeders themselves (binomial sign test, 5/8 chose nest option on first visit, *P* = 0.73).

Across their first visits juveniles showed no preference for a side within sites, and preference also did not differ between sites (Fisher's exact test: Site 1 = 10/24 visits to RHS, Site 2 = 15/25 visits to RHS, *P* = 0.26). For comparison, adults also showed no preference at either site (Fisher's exact test: Site 1 = 2/12 visits to RHS, Site 2 = 6/12 visits to RHS, *P* = 0.19; 4 parents [3 males, 1 female] from side-choice feeder nests visited, but none chose their nest side on first visit). Peers also had little influence on side choice during first visits. Most juveniles first visited on day 1 or 2 (35/49, 71%), and half were within 2 minutes of the previous hihi (22/47 47%; the first visitors to each site are excluded). However, hihi only chose the same side as the previous bird 45% of the time (21/47) and were not more likely to copy if visits were closer together (null model ranked higher than one including latency from previous bird's visit; Supplementary Table 4.2).

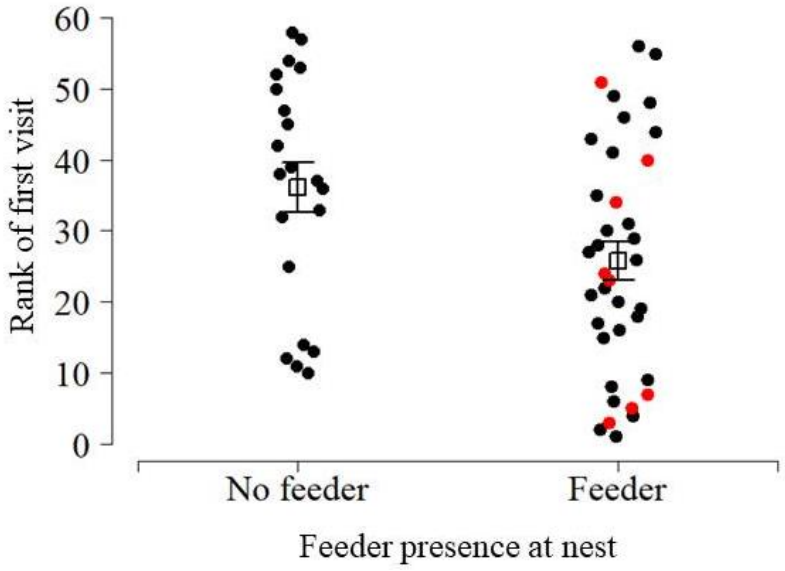
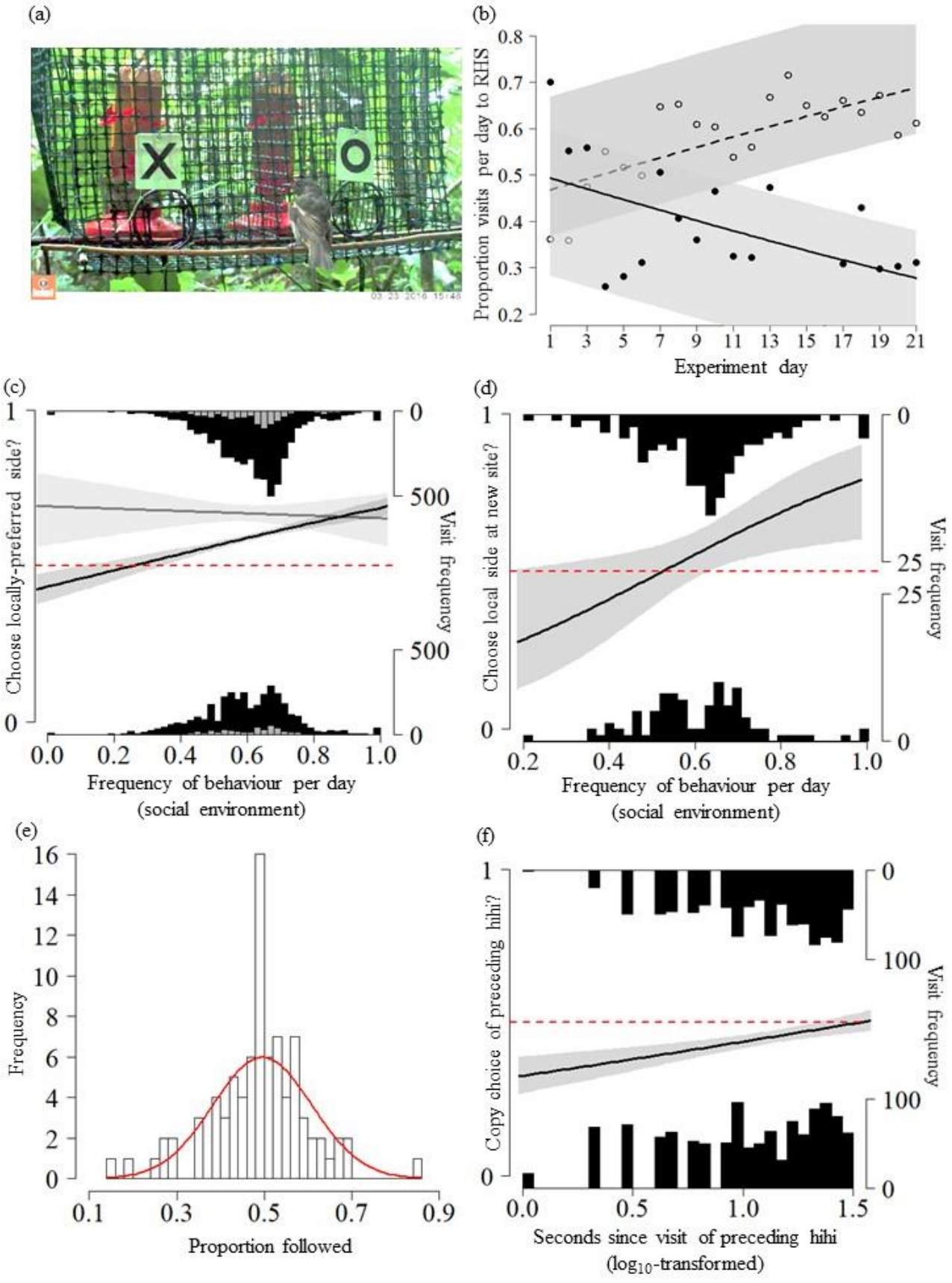



**Figure 4.4.** Ranks of first visits to group site feeders for juveniles from nests with no feeder and nests with feeders. Red points depict juveniles from nests where parents did not use feeders. Open squares depict mean rank (± standard error).

**Ongoing visits: did juveniles copy peers?**

Despite both sides being equally rewarding, hihi groups developed a local preference for one side as the experiment progressed, but in the opposite direction at the two sites (*N* visits = 10049; the only model with ΔAICc < 2 included experiment day*site; effect = -0.08±0.01, 95% CI = -0.09 – -0.07; Figure 4.5a, b; Supplementary Table 4.3a). This was not because of assortment of juveniles from the different side-choice nests as they did not differ in their proportion of visits at the two sites (no difference in proportion of visits juveniles from each group made at Site 1; Wilcoxon rank sum test: $W = 33.5$, $P = 0.87$) and did not maintain a significant preference across their visits within each site (null model ranked highest; Supplementary Table 4.3b). In all birds, side chosen on first visit did not predict a hihi's overall side preference in either site (Fisher's exact test: Site 1: 23/36 hihi maintained a preference for the same side chosen on first visit; Site 2: 23/38 maintained a preference; $P = 0.81$). For all juveniles ($N = 49$), but not adults ($N = 25$), side choice was best explained by the strength of the group's preference that day for the locally-preferred side (age*social environment, Table 4.1a; Figure 4.5c; Supplementary Table 4.4a). By comparison, adults developed a stronger preference over days compared to juveniles (visit day*age, Table 4.1a; Supplementary Table 4.4a). There was a non-significant trend for side choice in both adults and juveniles to follow the group's preference more strongly later in the day (Table 4.1a; Supplementary Table 4.4a), but there was no evidence that having more associates in the network affected side choice (no effect of degree on choosing locally preferred side: Table 4.1a; Supplementary Table 4.4a).

After changing sites, juveniles also responded to the preferences of the new group. Juveniles were more likely to choose the local side when it was used most by the other group that day (Figure 4.5d, Table 4.1b, Supplementary Table 4.4b). This did not, however, vary with previous personal experience: side choice was not influenced by a stronger preference for the opposite side at their previous site (Table 4.1b, Supplementary Table 4.4b), and there was no effect of visit day or the number of times they had changed site (Table 4.1b). Time of day now had no effect on side choice (Table 4.1b; Supplementary Table 4.4b). Juveniles likely had the opportunity to observe multiple birds to assess group preference between leaving one site and using the feeder in the next, as the time between visiting feeders in different sites was longer than one hour in 70% of all site changes (median = 1.8 hours: IQR = 15.8; Supplementary Figure 4.1a) and a null GLMM model investigating variation in inter-site times was ranked higher than a model including experiment day (Supplementary Figure 4.1b; Supplementary Table 4.5a). Juveniles changed sites more times as the experiment progressed (effect of experiment day on number of changes per day = 0.06±0.01, 95% CI = 0.03 – 0.08; Supplementary Figure 4.1c; Supplementary Table 4.5b), so they could have encountered peers at both sites, multiple times per day. Finally, juveniles rarely followed an individual that had also changed sites (10/242 site changes), suggesting they were integrating into a group and not moving in flocks between feeders.




*(Figure caption on following page)*

**Figure 4.5.** (a) juvenile hihi visiting group site feeder; (b) proportion of visits recorded per day to RHS at group feeders (Site 1 = dashed line; Site 2 = solid line), which shows how preference for one side of the feeders changed across the experiment; (c) likelihood that juveniles (black line) and adults (grey line) chose the local side (yes = 1, no = 0), depending on frequency its use by other hihi that day. The frequency at which hihi chose either side depending on social environment strength is shown by the histograms (black = juveniles; grey = adults). Shows that side choice depended on social group preference in juveniles, but not adults; (d) likelihood that juvenile hihi (black line) chose the local side when they changed between sites (yes = 1, no = 0), depending on frequency its use by other hihi that day. Frequency at which juveniles chose either side depending on social environment strength is depicted with histograms. Shows that juveniles copied group preference when they moved to a new site; (e) Frequencies of the proportion of visits by each individual where their side choice was copied by the following hihi, where red line represents normal distribution for reference. Shows that most individuals were only copied by the next bird on 50% of visits; (f) Likelihood that hihi chose the same side as the previous bird (yes = 1, no = 0), for visits under 30 seconds apart. Frequency that hihi chose either side depending on seconds since preceding visits is depicted with histograms. Shows that hihi were less likely to copy the preceding bird when they visited very soon after. All predicted model estimates and 95% confidence intervals (grey areas) come from top-ranked models. Dashed red lines indicate 50% likelihood of copying.

**Table 4.1.** Effect sizes and 95% confidence intervals for predictors included in the top model set ($\Delta$AICc < 2) analysing likelihood that hihi chose the locally-preferred side for (a) all visits and (b) when juveniles changed sites. Group preference = proportion end-preferred side was used by other hihi that day; focal degree of visiting bird calculated from the social network collected prior to side choice feeder setup.

| | **Predictor** | **Effect** | **95% CI** |
|---|---|---|---|
| (a) All visits to group feeders | Group preference*age (juvenile) | 1.66 ± 0.67 | 0.35 – 2.97 |
| | Visit day*age (juvenile) | -0.05 ± 0.02 | -0.08 – -0.02 |
| | Time of day (hours) | 0.01 ± 0.01 | 0.00 – 0.02 |
| | Focal degree | -0.23 ± 0.21 | -0.65 – 0.18 |
| (b) Visits when juveniles changed sites | Group preference | 2.78 ± 1.32 | 0.20 – 5.37 |
| | Visit day | 0.04 ± 0.03 | -0.02 – 0.11 |
| | Time of day (hours) | -0.06 ± 0.05 | -0.16 – 0.03 |
| | Site change number | -0.03 ± 0.03 | -0.09 – 0.03 |
| | Previous day preference | 0.07 ± 0.80 | -1.50 – 1.64 |

Although side choice was affected by the group's preferences, hihi did not appear to copy particular individuals. Very few birds had a high (or low) probability of being copied, and most individuals were copied on approximately half their visits (Figure 4.5e; mean proportion copied = 0.50; 74% of individuals fell within 1 standard deviation of the mean). Adults and juveniles were equally likely to copy (included in models with ΔAICc < 2 but effect = -0.07 ± 0.10; 95% CI = -0.26 – 0.12) and did not change their behaviour if they were more social, according to the age of the previous individual, nor if they were more familiar with that preceding bird (Supplementary Table 4.6a). Instead, the only significant predictors were time between visits, as individuals became less likely to copy the previous bird when their visits were closer together (effect size of increasing time since preceding bird's visit = 0.24 ± 0.04; 95% CI = 0.16 – 0.31; Supplementary Table 4.6a), and a stronger group preference that day (effect size = 0.65 ± 0.19; 95% CI = 0.27 – 1.03). The effect of time was stronger if the previous hihi was still at the feeder, as we re-analysed the top models but only included visits fewer than 30 seconds apart (Figure 4.5f; median time hihi spent inside feeders during 345 observations of feeding visits = 30s, IQR = 0; effect = 0.54±0.13, 95% CI = 0.28 – 0.80). Similarly, whenever juveniles changed sites no predictor significantly affected their likelihood of copying (null model ranked highest; Supplementary Table 4.6b).

## *Discussion*

Here, we demonstrated that social experiences with parents and peers in early life affected the foraging behaviour of young passerine birds. When given a choice between accessing a feeder on the left or on the right-hand side, recently-fledged hihi chose the same side as their parents. Furthermore, once they became independent and formed groups, juveniles that had previously encountered feeders with parents used a novel feeder before naïve birds. However, when encountering a feeder with a similar side-choice (but both sides were now equally rewarding), they did not maintain their parents' preference. Instead, choice was initially random but over time all juveniles updated their choice in response to their peers' behaviour. Juveniles paid more attention to this social information than adults did, but did not copy particular individuals. Consequently, the frequency of visits to one side of the feeder increased across the experiment, and to opposite sides at two different sites. Finally, individuals that switched between sites were more likely to match the locally-preferred option as more local birds chose that side.

Some behaviours are transmitted from parents to offspring directly through imitation or teaching (Thornton, 2006; van de Waal, Bshary and Whiten, 2014; Iwata *et al.*, 2017) but time with parents can also facilitate learning new behaviour in other ways, such as promoting individual trial-and-error learning (Truskanov and Lotem, 2017). Our experiment may also demonstrate an indirect effect of time spent with parents on juvenile foraging behaviour. In hihi, the presence of a feeder at the nest site during parental care meant juveniles were quicker to use feeders than those that had never encountered them before. However, more specific experience of interacting with the feeder stimulus did not influence behaviour, as side choice at feeders was random irrespective of whether juveniles had experienced a

side-choice before. Furthermore, feeder juveniles' responses were not determined by parents' use of feeders at their nests. This suggests young hihi did not need to directly observe parent behaviour during early life, but instead they learned a generalised stimulus (feeder) response through exposure to the feeder object itself. Similar results have also been found in parrots (*Amazona amazonica*), where interactions with parents did not determine later responses to objects, but the presence of these objects during parental care did (Fox and Millam, 2004). Thus, lasting effects of time with parents may be subtle, and changes in behaviour can result from indirect influences.

By contrast, we found that young hihi copied their peers once independent while adults did not respond to the behaviour of others. Due to their inexperience, juveniles may rely more than adults on social information to determine behaviour (Laland, 2004; Kendal *et al.*, 2005; Kendal, Coolen and Laland, 2009). Further, young hihi also altered their choices based on the overall collective behaviour of the group rather than specific individuals, as there was little evidence that familiarity and sociality affected hihi behaviour. Although individual-level familiarity or number of associates is important for information dissemination in some contexts (Aplin *et al.*, 2012; Atton and Galef, 2014; Guillette, Scott and Healy, 2016; Ramakers *et al.*, 2016), they may be less crucial when using collective information provided by groups. Generally, copying the predominant behaviour of groups rather than specific individuals is thought to help animals overcome some pitfalls of using social information (King and Cowlishaw, 2007; Conradt and Roper, 2005; but see Giraldeau, Valone and Templeton, 2002), such as the risk of copying misinformed individuals (Curio, Ernst and Vieth, 1978; Ward and Zahavi, 2008; Pruitt *et al.*, 2016). If juveniles also have limited experience to judge reliability from different sources, then groups may provide a more complete picture of behavioural responses to the current environment (Clark and Mangel, 1984; Conradt and Roper, 2005). This could explain why we found little evidence that familiarity or degree, both specifically determined from visits to the feeders, affected hihi behaviour.

When paying attention to the collective behaviour of peers, animals may respond to small changes in the frequency of behaviour in groups to alter their own preferences and conform. Although there has been debate surrounding how to define conformity (for discussion, see Aplin *et al.*, 2015a; van Leeuwen *et al.*, 2015, 2016; Whiten and van de Waal, 2016), a general rule is that conforming animals tend to prefer a common behavioural option in a group, even if they have experience of alternative options (de Waal, 2013). Within the past 10 years behavioural conformity has been suggested to occur in taxa from invertebrates to humans, which highlights a widespread tendency for animals to copy the behaviour of others (birds: Aplin et al., 2015b; invertebrates: Fürtbauer & Fry, 2018; fish: Pike & Laland, 2010; primates, including humans: Haun, van Leeuwen, & Edelson, 2013; van de Waal et al., 2013; van de Waal, van Schaik, & Whiten, 2017; but see van Leeuwen et al., 2013). In support of this, juvenile hihi developed a preference for one feeder side which was driven more strongly by the behaviour of others than personal learning. Previous studies have further suggested animals quickly conform to traditions in new groups (van de Waal, Borgeaud and Whiten, 2013), and we also found evidence that copying was localised to the extent that juvenile hihi switched their behaviour when moving between groups with opposite preferences.

We acknowledge that with only two replicates of the feeder experiment in groups, it is possible that side choice patterns could have developed as a result of environmental effects (for example, surrounding vegetation). However, several lines of evidence suggest this was unlikely. Firstly, initial side choice was random at both feeders, suggesting no effect of an immediate bias. Secondly, the progressive changes in side choice were similar (albeit in the opposite direction) at both feeders and it is unlikely that both feeders would have followed similar changes if there was an effect of some environmental aspect. Furthermore, side choice did not appear to be habit-driven (Pesendorfer *et al.*, 2009) as first side choices did not predict overall individual preference. Finally, the effect of social environment was stronger than that of visit day, especially when juveniles moved sites: here, there was no significant effect of day, only an effect group preference. This suggested that an individual did not increase its preference for one side purely as a result of visiting the same feeder repeatedly over days. Instead, juvenile hihi paid attention to peers even with their own experience of the non-preferred side and when the cost of choosing that side was small. Overall, this suggests that juvenile hihi were copying predominant behaviours to conform to the group preference and adjusted their choices quickly irrespective of prior experience. This is only the second study (as far as we know) to demonstrate conformity patterns in wild birds (Aplin *et al.*, 2015b).

While conforming can perpetuate behavioural biases in populations under certain conditions, emerging evidence shows that when conforming becomes a suboptimal strategy, animals reduce their tendency to copy (Aplin, Sheldon and McElreath, 2017). We also found that hihi were less likely to copy when using feeders at very similar times, and instead used the equally-rewarding alternate side. This could be a way to avoid queuing before feeding themselves, and maintain an optimal foraging intake (Milinski, 1982; Krebs and Inman, 1992). Even when animals have a propensity to disregard their own experience and copy the behaviours of others, they still pay attention to small trade-offs between competitive interactions and social learning strategies (Laland, 2004). Conformity in natural populations where there is social information use, competition, and/or resources of similar payoff (as in our experiment) may never result in a strong sigmoidal relationship between frequency of behaviour and likelihood of copying seen in previous studies (Aplin *et al.*, 2015a, 2015b). Flexible use of conformist strategies under different levels of payoffs has only just begun to be considered (van Leeuwen *et al.*, 2013; Aplin, Sheldon and McElreath, 2017), but here we suggest using social information to conform may particularly benefit naïve animals in less competitive environments.

Social information use is thought to play a key role in shaping ecological processes contributing to population stability, such as finding food, avoiding predation, and disease transmission (Blanchet, Clobert and Danchin, 2010). Sociality can be important to survival of juveniles in some species (for example feral horses, *Equus callabus* (Nuñez, Adelman and Rubenstein, 2015); also see Chapter 5). Therefore, clarifying the importance of juvenile groups for behaviour may help understand what influences survival during conservations translocations (Cox *et al.*, 2014). Young hihi are often translocated to new sites to establish or supplement populations, so if peers are important *in situ* on

Tiritiri Matangi Island, they may become more important at new sites or in environments where the risks of learning alone increase (Kendal *et al.*, 2005; Webster and Laland, 2008; Rendell *et al.*, 2010). However, because young hihi copied group behaviour (and did not copy according to familiarity), this could suggest that the specific identities of peers are not crucial to help them survive the critical post-release period. Ultimately, copying groups not individuals could allow juveniles to conform quickly to new environments, if paying attention to whichever individuals are present at the time is a way of attaining information about the current environment (Hatch and Lefebvre, 1997; Ramakers *et al.*, 2016). Testing how groups change following translocations will further help understand the value of the group as a whole to juveniles of threatened species.

# CHAPTER

# 5

# Changes in social groups across reintroductions and effects on post-release survival

*Data collection for this chapter assisted by: Mhairi McCready (MM) and Caitlin Andrews (CA)*
*Hihi translocation led by: Kevin Parker*
*I am grateful to Matthew Silk for advice on social network analysis for this chapter*

Reintroductions are essential to many conservation programmes, and thus much research has focussed on understanding what determines the success of these translocation interventions. However, while reintroductions disrupt both the abiotic and social environments, there has been less focus on the consequences of social disruption. Therefore, here we investigate if moving familiar social groups may help animals (particularly naïve juveniles) adjust to their new environment and increase the chances of population establishment. We used social network analysis to study changes in group composition and individual sociality across a reintroduction of 40 juvenile hihi (*Notiomystis cincta*), a threatened New Zealand passerine. We collected observations of groups before a translocation to explore whether social behaviour before the reintroduction predicted associations after, and whether reintroduction influenced individual sociality (degree). We also assessed whether grouping familiar birds during temporary captivity in aviaries maintained group structure and individual sociality, compared to our normal translocation method (aviaries of random familiarity). Following release, we measured if survival depended on how individual sociality had changed. By comparing these analyses with birds that remained at the source site, we found that translocation lead to re-assortment of groups: non-translocated birds maintained their groups, but translocated juveniles formed groups with both familiar and unfamiliar birds. Aviary holding did not improve group cohesion; instead, juveniles were less likely to associate with aviary-mates. Finally, we found that translocated juveniles that lost the most associates experienced a small but significant tendency for higher mortality. This suggests sociality loss may have represented a disruption that affected their ability to adapt to a new site.

## Introduction

Reintroduction, returning species to parts of their range where they have become extinct (IUCN/SSC, 2013), is important for many conservation programmes (Armstrong and Seddon, 2008). The process of moving animals to a new site ("translocation" (IUCN/SSC, 2013)) and overcoming post-release effects during "establishment" (IUCN/SSC, 2013) are critical to the success of reintroductions (Fischer and Lindenmayer, 2000; Bennett *et al.*, 2012; Parker *et al.*, 2012; Miskelly and Powlesland, 2013; Armstrong *et al.*, 2017). Novelty of the post-release environment appears to be a major challenge to survival because animals need to avoid starvation and predation with little personal experience of the release site (Letty *et al.*, 2003; Pinter-Wollman, Isbell and Hart, 2009; Batson, Abbott and Richardson, 2015). Thus, key remaining questions in reintroduction biology centre around how animals adjust successfully to their new environment and what can increase their post-release survival (Anthony and Blumstein, 2000; Armstrong and Seddon, 2008).

Reintroductions change the abiotic environment, but also the social environment when the founding group of animals represents a subsample of a larger original population (Ewen, Armstrong, Parker, *et al.*, 2012). The composition of groups may be important for establishment (Anthony and Blumstein, 2000; Clarke, Boulton and Clarke, 2003; Armstrong and Seddon, 2008; IUCN/SSC, 2013) because it can affect how animals adjust behaviour as a first-response mechanism to a new environment (Wong and Candolin, 2014). Animals may prefer to associate with and learn from familiar peers when finding food or avoiding predation (Atton & Galef, 2014; Lachlan, Crooks, & Laland, 1998; Schwab, Bugnyar, Schloegl, & Kotrschal, 2008; but see Ramakers, Dechmann, Page, & O'Mara, 2016) and in novel environments, collective group knowledge may become more important because it can offset each individuals' limited personal experience (King and Cowlishaw, 2007; Pinter-Wollman, Isbell and Hart, 2009). Associations can also affect the likelihood that animals disperse post-release, as more cohesive groups are less likely to split up (Blumstein, Wey and Tang, 2009; Snijders *et al.*, 2017). Therefore, if animals lose previous social connections during reintroductions there may be consequences for population stability, for both the translocated population as well as the remaining source population (Blanchet, Clobert and Danchin, 2010; Pinter-Wollman *et al.*, 2013).

To understand how group structure and familiarity impacts on translocation success, we therefore first need to determine if groups remain together when they are moved to a new site. One challenge in wild animal groups is there may be limited knowledge of familiarity before translocation. For example, studies in New Zealand bird species (tīeke/saddleback, *Philesturnus carunculatus rufusater*; toutouwai/North Island robin, *Petroica longipes*) and howler monkeys (*Alouatta seniculus*) found that pre-capture familiarity was not maintained over translocation (Armstrong, 1995; Armstrong and Craig, 1995; Richard-Hansen, Vié and De Thoisy, 2000). However, these species are territorial, and the studies also defined familiarity from short-term binary measures (individuals in the same place upon capture were "familiar",

versus “non-familiar”). When longer-term measures of familiarity have been used for more social groups (such as families or colonies) there is evidence that group composition remains similar before and after reintroduction (Clarke, Boulton and Clarke, 2003; Shier, 2006; Pinter-Wollman, Isbell and Hart, 2009) and that maintaining groups results in higher post-release survival (Shier, 2006). Therefore, capturing group familiarity over a longer time period for social species may be required to assess the importance of maintaining or disrupting relationships over translocations.

Along with the identity of members of a social group, an animal’s number of social connections may also affect how well it adjusts in a novel environment. Some individuals have many associates while others have few (Krause, Lusseau and James, 2009); generally, more social animals acquire new behaviours more quickly, likely because they have more potential sources of information to use (Aplin *et al.*, 2012; Snijders *et al.*, 2014). In a new and unknown environment (such as a release site), where animals need to acquire new information (for example, to discover new foraging sites), having many social connections may therefore be beneficial. Number of social connections may be especially important if animals are particularly reliant on learning with others, for example juveniles who need to overcome their own limited personal experience (Chapter 2; Chapter 4; Letty, Marchandeau and Aubineau, 2007; Nuñez, Adelman and Rubenstein, 2015). However, by disrupting the social environment, reintroductions may change an individual’s associations. Little is yet known about individual-level consistency in sociality, and there is limited research exploring the consequences of extensive social disruption (Nuñez, Adelman and Rubenstein, 2015; Firth *et al.*, 2017). However, evidence from one study suggests that animals (juvenile feral horses *Equus caballus*) with more social connections may better survive changes in groups such as loss of members, compared to less social peers (Nuñez, Adelman and Rubenstein, 2015); this may be because they lose proportionally fewer associates. Individual sociality may therefore also be important for population stability during establishment (Modlmeier *et al.*, 2014; Snijders *et al.*, 2017).

Familiarity may also develop between previously unfamiliar individuals if animals are held in temporary captivity for disease screening or to acclimate them to the release site (IUCN/SSC, 2013; Batson, Abbott and Richardson, 2015). This has implications for both group structure and individual sociality, if it promotes cohesion and increases associations. In some social species such as African wild dogs (*Lycaon pictus*) and lions (*Panthera leo*), groups formed during pre-release integration were more likely to remain together post-release, while translocations with non-integrated individuals failed (Gusset, Slotow and Somers, 2006; Hunter *et al.*, 2007). However, there also are cases where temporary captivity did not significantly improve group cohesion over immediately-released groups (Clarke, Boulton and Clarke, 2003), or groups disbanded even if translocated together (Fritts, Paul and Mech, 1984). Further, there are other implications of delayed release and in some species it can lead to reduced post-release survival (Castro *et al.*, 1994; Richardson *et al.*, 2013) or increased stress (Batson *et al.*, 2017). Thus, the benefits of temporary captivity are likely species-specific (Moseby, Hill and Lavery, 2014) and a clear understanding of a variety of different advantages and disadvantages of this strategy (including social cohesion) are important to evaluate its use for the species in question (IUCN/SSC, 2013).

Social network analysis provides a way to examine the detailed relative changes in group composition and individual social traits, but as yet has had limited application to studies of conservation value (Wey *et al.*, 2008; Snijders *et al.*, 2017). By collecting repeated observations of co-occurring individuals, we can determine relative familiarity across a population and define "communities" of frequently co-occurring individuals (Krause *et al.*, 2015). We can also calculate individual-level metrics, such as number of associates ("degree centrality") (Krause *et al.*, 2015). Following translocation, we can assess changes in network structure and individual metrics (Snijders *et al.*, 2017). If we need to identify particular social characteristics of groups or individuals that are beneficial to reintroductions, social network analysis could inform conservation practice. Further, using translocation as an experimental platform can help us test how group- and individual-level network changes impact on population stability, including survival, information flow and disease dynamics (Snijders *et al.*, 2017). As such, opportunities where we can implement social network analysis when testing effects of changing social groups in species of conservation concern provide valuable examples that both inform conservation practice, and help understand the broader ecological and evolutionary consequences of social networks (Pinter-Wollman *et al.*, 2013; Kurvers *et al.*, 2014; Formica *et al.*, 2016; Firth *et al.*, 2017).

Here, we use a translocation of hihi (stitchbird, *Notiomystis cincta*) to test fitness effects of network structure, and assess whether maintaining sociality can improve the outcome of a translocation. This species is a threatened New Zealand passerine (Birdlife International, 2017) which was once widespread across the North Island. Following the introduction of non-native predators when humans arrived in New Zealand, hihi became restricted to a single off-shore island (Hauturu-o-Toi/Little Barrier Island). Since the 1980s a major aim for conservation of this species has been to establish re-introduced populations in predator-controlled areas, and the most recent hihi translocations have involved moving juvenile birds. This cohort appears to be particularly social: juveniles form groups for several months at the end of the breeding season and interact, for example with "play"-like behaviour and allopreening (Chapter 3). However, it is unknown whether translocation alters these social groups or what the consequences may be for establishment of populations. We used the opportunity of a translocation in 2017 to test our predictions that: (1) translocated hihi will group with more familiar individuals from either before the translocation, or based on who they were held with during temporary captivity; (2) individuals will remain consistent in their sociality before and after translocation; and (3) any changes in social behaviour will affect survival after translocation.

## Methods

### SOURCE AND RELEASE SITE

In 2017 we reintroduced hihi to Rotokare Scenic Reserve ("release site", 39°27'15.4"S 174°24'33.0"E) from Tiritiri Matangi Island ("source site", 36°36'00.7"S 174°53'21.7"E). The source site is a 220ha island scientific reserve of replanted and remnant native fauna which is free of non-native mammalian predators. Hihi were reintroduced to the island in 1995 (Armstrong and Ewen, 2001), and the population (numbering c. 270 in 2017) is now the main source of birds for ongoing translocations to other sites. The release site (230ha, including a 17.8ha lake) is a mainland site of old-growth native forest surrounded by a fence that excludes non-native mammalian predators. Hihi had been locally extinct at this site and in the surrounding region for c.130 years prior to the reintroduction (Angher, 1984).

### DEFINING FAMILIARITY BEFORE TRANSLOCATION

Between 17th January – 19th March we collected 229 hours of observational surveys of 105 individuals to determine familiarity at the source site before translocation. To observe as many juveniles as possible we carried out surveys in nine forested gullies (including the three main group sites occupied by juveniles that year, see Chapter 3) and at six permanent supplementary feeding stations on the island. This ensured we observed associations among juveniles commonly seen at group sites and also associations with the few juveniles that did not frequent these sites (17/108 juveniles were never seen at group sites). During each one-hour survey we recorded the identities of all juveniles seen within a 10-metre radius of the observer (VF). All hihi have an individual combination of coloured leg rings (applied to nestlings during routine nest monitoring) so each could be identified by sight. We assigned juveniles to the geographical location where they were observed: 40 birds were only ever recorded in the northernmost groups ("north"), 16 at the southern end of the island ("south") and the remaining 49 mixed between the two (mixed).

Next, we constructed a "group-by-individual" (GBI) matrix where a group comprised any juveniles seen within 15 minutes of the preceding bird. If we did not see any birds during this time, we considered the next juveniles encountered to be part of a new group. We used this "gambit of the group" approach (Whitehead, 2008) due to practical limitations from needing to incorporate social network data collection after translocation into the post-release monitoring of the population (see below), and recorded network before- and after-translocation using the same technique to ensure they were comparable (Castles *et al.*, 2014). However, the 15-minute window was determined as a suitable cut-off to describe hihi associations based on previous observations and analysis of hihi social groups where the majority of groups (and individuals) were recorded in an area for a maximum of 15 minutes (Appendix 2.1). Using

the GBI, we built a weighted association network in R (version 3.5.0) (R Core Team, 2017) using the "get_network" function in the R package asnipe (version 1.1.9) (Farine, 2013). Weighted networks provided a more detailed measure of familiarity rather than binary familiar/unfamiliar: each "edge" connecting two juveniles represented at least one co-occurrence in a group, so repeated co-occurrences (and stronger edge weights) would indicate that juveniles were more familiar. We detected "communities" of frequently co-occurring individuals in the network using the community detection algorithm of Clauset et al. (2004) implemented with the "fastgreedy.community" function (igraph R package version 1.0.9, (Csárdi and Nepusz, 2006)). We ensured that assigned communities were robust following the method of Shizuka & Farine (2016): we generated bootstrapped replicates of the observed network by resampling observations of groups before translocation, and in each bootstrapped network we calculated assortment by the community assigned to each juvenile from the observed network. This allowed us to determine if the observed community structure was robust compared to random expectation by calculating the metric $r_{comm}$. If $r_{comm}$ = 1, all replicated networks result in the same community structure as the observed network; conversely, $r_{comm}$ = 0 means that assignments are random compared to original assigned communities ($r_{comm}$ > 0.5 is considered "robust" (Shizuka and Farine, 2016)). We assigned each juvenile a number (1-6) corresponding to its network community.

**TRANSLOCATION**

On 27th – 28th March, 40 hihi were caught in mist nets or by capturing birds individually as they entered permanent supplementary feeding stations at locations across the source site. We did not control for individual differences in selectivity (likelihood of capture could, for example, depend on boldness (Madden and Whiteside, 2014)), but the same technique has been used across many previous hihi translocations. Therefore, the questions we were asking remained relevant to inform management for this conservation action. After capture, each bird was transported individually to be processed immediately for disease screening (Ewen, Armstrong, Empson, *et al.*, 2012). After processing, each bird was released into one of three pre-existing aviaries which have been used in many translocations from the source site (each measuring approximately 5x3x2.5 metres). The aviaries were one large enclosure divided into three flights and filled with dense natural vegetation that limited visual contact between aviaries (aviaries were therefore not in auditory isolation from each other or free-living birds). Each juvenile was assigned to an aviary based on its community in the network before translocation: one aviary contained birds from one community only ("familiar" group), while the remaining two aviaries contained birds from all communities ("mixed" groups, the normal management used in previous hihi translocations). We ensured that mixing juveniles from different communities also included spatially-separated birds (i.e. only detected in northern or southern survey locations) that had little chance to interact prior to capture.

All birds for translocation were caught within 24 hours, then kept in the aviaries for four further days while samples were processed for disease screening. Each aviary held equal numbers of birds. During holding we provided supplementary food twice daily, using the same range of food used in previous

successful hihi translocations (Ewen *et al.*, 2018). On the evening of the 1st April, hihi were re-caught from the aviaries, health-checked, and transferred to translocation boxes (five hihi per box). We transported all birds at the same time from the source site to the release site, overnight (by boat then van) to minimise stress for the birds. All hihi were released successfully the following morning (2nd April).

**DEFINING FAMILIARITY AFTER TRANSLOCATION**

We recorded associations at both the release site and source site from 3rd April – 3rd June 2017 in a similar manner as before translocation. However, as hihi were expected to disperse across the release site and not be fixed to locations following the translocation, we walked monitoring tracks at both sites to locate juveniles (by MM and CA at the release site: 300 observation hours, 38 individuals; by VF at the source site: 100 observation hours, 40 individuals). We accounted for potential effects of different levels of re-sighting on social network measures (both before and after translocation) in our later analyses. All three observers had similar experience of observing hihi as part of the standard monitoring of the source population. Whenever we encountered a juvenile, we noted the bird's colour ring combination, the time it was first encountered (to nearest minute) and the time it left the area too quickly for us to follow. If we saw new individuals during the same time, we also noted their identity, entry time, and exit time. Using the same method at the release site and at the source site meant we could compare changes in social patterns in translocated juveniles to a group that had experienced network disruption while remaining in the same location. We constructed networks for source and release sites separately, using the same method as before translocation.

Post-release survival population surveys were conducted by MM at the release site every month between May – September 2017, and in March 2018 following the first breeding season of this new population. During each survey, MM walked monitoring tracks (a subset, alternated between surveys) across the release site for 40 hours over five days. Using this method meant birds could be detected by their calls across the entire site in each survey, located, and visually identified using binoculars. Partially-identified birds (for example, incomplete ring combinations) were discounted to limit misidentification. For each translocated hihi, we created encounter histories which represented each bird's presence ("1", seen) or absence ("0", not seen) in each successive survey or "time point". All individuals were assigned a "1" in time point 1 when they were released into the new site in April 2017 (all hihi were released successfully). Thus, an example encounter history would be "1110000", where an individual was released at time point 1, seen in the surveys at time points 2 and 3, and then not seen again. Population surveys were also conducted at the source site by MM in September 2017 and February 2018 using the same method. For non-translocated hihi, we generated encounter histories from presence/absence in April 2017 observations, May 2017 observations, plus the two censuses. Time point 1 in these encounter histories (when all individuals were considered present and assigned "1") was immediately before the translocation (March 2017). We used these data to investigate links between changes in social networks and survival for translocated birds, which we might expect if losing social connections was disruptive or stressful for hihi, and to compare their survival to non-translocated hihi.

## DATA ANALYSIS

### Did translocation change group associations?

Social network analysis was conducted in R. We first tested if hihi grouped after the translocation according to familiarity based on (i) geographic distribution before translocation (north locations only, south locations only, mixed sightings); (ii) social network community before translocation (community 1-6); and (iii) aviary during the translocation ("1" (mixed); "2" (familiar); "3" (mixed)). For each analysis, we calculated the distribution of network edge weights and the assortativity coefficient (*r*, a value from +1 for total disassociation, to +1 for total association) to describe the strength of associations between juveniles based on our categorical measures (using the R package assortnet (version 0.12) (Farine, 2014)). We compared the *r* value of our network to the r values of 1000 random networks generated using pre-network data permutations in asnipe, to test if familiar juveniles were statistically more likely to associate than random. Data-stream permutations account for differences in the number of observations between individuals when calculating network statistics (Farine and Whitehead, 2015; Farine, 2017), and comparisons with permuted networks is a more robust method for determining statistical significance because networks are inherently non-independent and violate the assumptions of statistical tests (Farine and Whitehead, 2015). Finally, we repeated assortment analyses based on distribution and communities for the source site network after translocation, as a comparison from non-translocated birds. All *P*-values generated by comparing with permuted networks are specified as $P_{rand}$.

### Did individuals remain consistent in their sociality?

Second, we investigated if relative individual sociality remained consistent following translocation by comparing between translocated and non-translocated individuals. For each individual in each network, we calculated a weighted degree centrality (degree) which explained both its number and strength of associations. As the population sizes of juveniles were different before and after translocation, we then ranked individuals by their degree within each network, and divided ranks by the size of each population so all ranks were bound between 0 and 1. Thus, if individual sociality was consistent we would expect an individual's rank to remain the same relative to others within their population. We assessed what predicted degree rank after translocation using a Generalised Linear Model (GLM) with a binomial distribution. Our predictors included degree rank before translocation, population (translocated or not translocated), and sex (translocations could affect male and female hihi differently (Armstrong *et al.*, 2002, 2017)). We included an interaction between degree rank before translocation and population type, because sociality could be affected more extensively if moved to a new site. Finally, we also included number of observations after translocation as a fixed effect to ensure variation in degree rank was not only due to differences in detection among individuals.

To assess whether maintaining familiar groups during capture for translocation affected individual sociality, we calculated each translocated juvenile's change in degree rank after translocation compared to before translocation (bound between -1 and 1; a negative value represented a decrease in social rank; a positive value was a rank gain). We used a Linear Model (LM) with rank change as the response. Our predictors included the aviary type each bird was housed in as "familiar" or "mixed"; initial exploratory analysis of the data (not presented) showed no variation in rank change between the two mixed aviaries so we only compared changes between the two different social management types. Degree before translocation was included in interaction with aviary type (effects of aviary could depend on sociality), and we also included sex as an additional parameter. For this analysis, we included number of observations both before and after translocation as fixed effects, because change in rank score (our response) could be dependent on variation in both number of observations. Again, we assessed significance of both analyses using data-stream permutations.

**Did social changes during the translocation affect survival?**

Finally, we used our encounter histories for translocated birds to estimate survival depending on change in degree rank (-1 – 1: covariate) and sex (male or female: grouping factor) in Program MARK (version 9.0) (White and Burnham, 1999). As all individuals were identifiable, we used a live-recaptures (Cormack-Jolly Seber, CJS) analysis to estimate survival ($\Phi$) and quantify re-sighting ($\rho$) to ensure survival was not confounded by varying re-sighting likelihoods between individuals. To ensure models explained variation in the data accurately, we first conducted a goodness-of-fit (GOF) test on a fully time- and group-dependent starting model, by calculating median ĉ as an estimate of overdispersion. We did not include covariates in this starting model as there is currently no method for GOF testing with covariates. The value for median ĉ = 1.30, which indicated a good fit of the data and so we corrected for the small level of overdispersion in further analyses. This meant we could accurately estimate $\Phi$ using:

**$\Phi$ (sex*degree rank change + time point*degree rank change)**

**$\rho$ (sex*degree rank change + time point*degree rank change)**

Here, we considered whether monthly survival was affected by the extent of change in rank degree after translocation compared to before translocation, explaining both loss and gain of associates relative to all other translocated juveniles. We considered rank change in interaction with sex, because this disruption could affect males and females differently, and time point (effects of social changes could vary across time). We accounted for variation in re-sighting likelihood with the same parameters. We did not analyse effects of degree rank change depending on aviary on survival, following evidence that there was no significant difference in degree rank change between aviary types (see Results).

We constructed a set of models with all combinations of predictors with and without the covariate, then ranked models by their corrected quasi-likelihood Akaike Information Criterion (QAICc, due to adjusting by median ĉ) values, which explain the model fit: a smaller QAICc value suggests the model better accounts for variation in the data. Any model less than 2 QAICc units from the top ranked-model was

considered equally well supported. If multiple models had ΔQAICc < 2, we used model averaging to calculate effect sizes and 95% confidence intervals depending on model weight (which explained relative likelihood of each model). Any parameter with a confidence interval that did not span zero was considered to have a significant effect.

We analysed survival in non-translocated birds depending on degree rank change and sex in the same manner, to provide a comparison from birds remaining at the source site. However, we could not combine both translocated and non-translocated birds in one survival analysis to explore interactions with site statistically, as the time points of the surveys differed. Our median ĉ value following GOF was 1.42 for the starting source site model, which we corrected for in our analyses.

## *Results*

### DID TRANSLOCATION CHANGE GROUP ASSOCIATIONS?

Before the translocation, juvenile hihi formed robust communities which represented preferred and avoided associations ($r_{comm}$ = 0.71). Juveniles that were not translocated continued to be seen in the same areas of the island and with group-mates from the same communities before translocation (location: $r$ = 0.12, $P_{rand}$ = 0.01, Table 5.1a, Figure 5.1; community: $r$ = 0.14, $P_{rand}$ = 0.01, Table 5.1b, Figure 5.2). However, translocated juveniles behaved differently: they did not group according to either their geographic location ($r$ = -0.04, $P_{rand}$ = 0.44, Table 5.2a, Figure 5.1) or community before translocation ($r$ = -0.01, $P_{rand}$ = 0.19, Table 5.2b, Figure 5.2). Additionally, translocated juveniles did not associate more strongly if they had shared an aviary, even when they had been familiar at the source site; in fact, there was a tendency for a weak disassociation by aviary (Table 5.2c; $r$ = -0.09, $P_{rand}$ = 0.04, Figure 5.2).

**Table 5.1.** Mixing matrices of association weights for hihi at the source site after the translocation based on (a) distribution before translocation at the source site (only in the "North", "South", or moved among the two "mixed"); and (b) network community before translocation (colours correspond to Figure 5.2a). $a_i^w$ are the row sums, $b_i^w$ are the column sums; due to rounding, sum values may not be exact. Tables are symmetrical, so only half of values are shown.

(a)

| Distribution | North | Mixed | South | $a_i^w$ |
|---|---|---|---|---|
| **North** | 0.21 | - | - | 0.41 |
| **Mixed** | 0.21 | 0.35 | - | 0.57 |
| **South** | 0.00 | 0.02 | 0.00 | 0.02 |
| **$b_i^w$** | 0.41 | 0.57 | 0.02 | 1.00 |

(b)

| Community | red | yellow | blue | green | $a_i^w$ |
|---|---|---|---|---|---|
| **red** | 0.07 | - | - | - | 0.29 |
| **yellow** | 0.15 | 0.19 | - | - | 0.42 |
| **blue** | 0.04 | 0.03 | 0.11 | - | 0.19 |
| **green** | 0.03 | 0.04 | 0.00 | 0.03 | 0.10 |
| **$b_i^w$** | 0.29 | 0.42 | 0.19 | 0.10 | 1.00 |

**Table 5.2.** Mixing matrices showing association weights for hihi at the release site after translocation based on (a) distribution at the source site before translocation; (b) network community before translocation (colours correspond to Figure 5.2a); and (c) aviary number and category during translocation. $a_i^w$ are the row sums, $b_i^w$ are the column sums; due to rounding, sum values may not be exact. Tables are symmetrical, hence only half of values are shown.

(a)

| Distribution | North | Mixed | South | $a_i^w$ |
|---|---|---|---|---|
| **North** | 0.11 | - | - | 0.35 |
| **Mixed** | 0.17 | 0.19 | - | 0.46 |
| **South** | 0.06 | 0.09 | 0.03 | 0.19 |
| **$b_i^w$** | 0.35 | 0.46 | 0.19 | 1.00 |

(b)

| Community | red | yellow | blue | green | purple | $a_i^w$ |
|---|---|---|---|---|---|---|
| **red** | 0.01 | - | - | - | - | 0.08 |
| **yellow** | 0.05 | 0.35 | - | - | - | 0.59 |
| **blue** | 0.02 | 0.19 | 0.10 | - | - | 0.32 |
| **green** | 0.00 | 0.00 | 0.00 | 0.00 | - | 0.00 |
| **purple** | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 |
| **$b_i^w$** | 0.08 | 0.59 | 0.32 | 0.00 | 0.00 | 1.00 |

(c)

| Aviary | 1 (mixed) | 2 (familiar) | 3 (mixed) | $a_i^w$ |
|---|---|---|---|---|
| **1 (mixed)** | 0.06 | - | - | 0.28 |
| **2 (familiar)** | 0.11 | 0.12 | - | 0.38 |
| **3 (mixed)** | 0.11 | 0.14 | 0.09 | 0.35 |
| **$b_i^w$** | 0.28 | 0.38 | 0.35 | 1.00 |

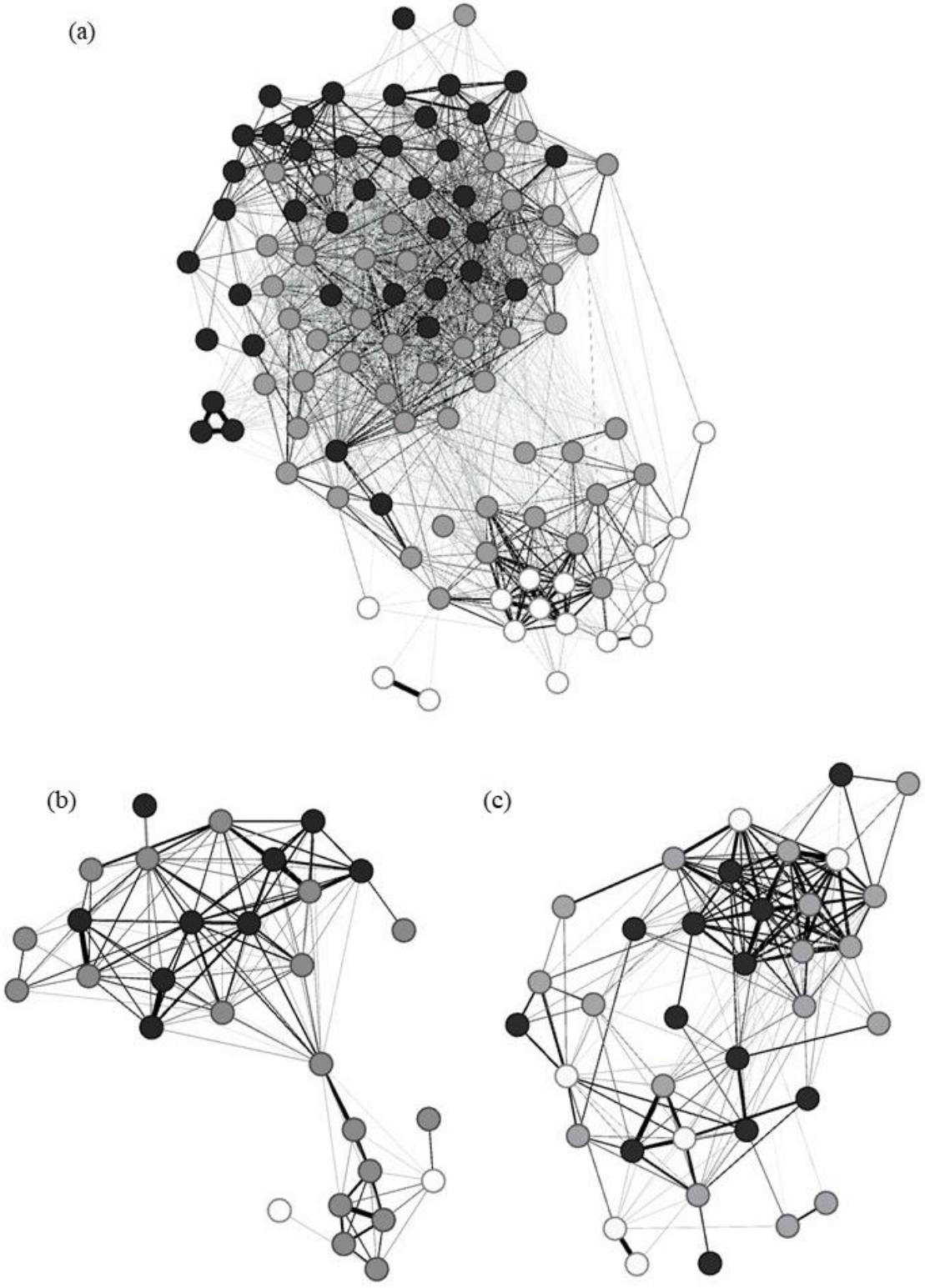



**Figure 5.1.** Hihi social networks (a) before translocation, and after translocation at (b) the source site, and (c) release site. Each node (circle) represents one hihi and the edges (lines) represent co-occurrence in a group. Edge width is proportional to association strength. Nodes in (a) are coloured by distribution at the source site (black = North; white = South; grey = mix). Nodes in (b) and (c) are coloured by the same distribution. Networks are arranged to minimise the length of edges between nodes which tends to cluster frequently-associating nodes together.

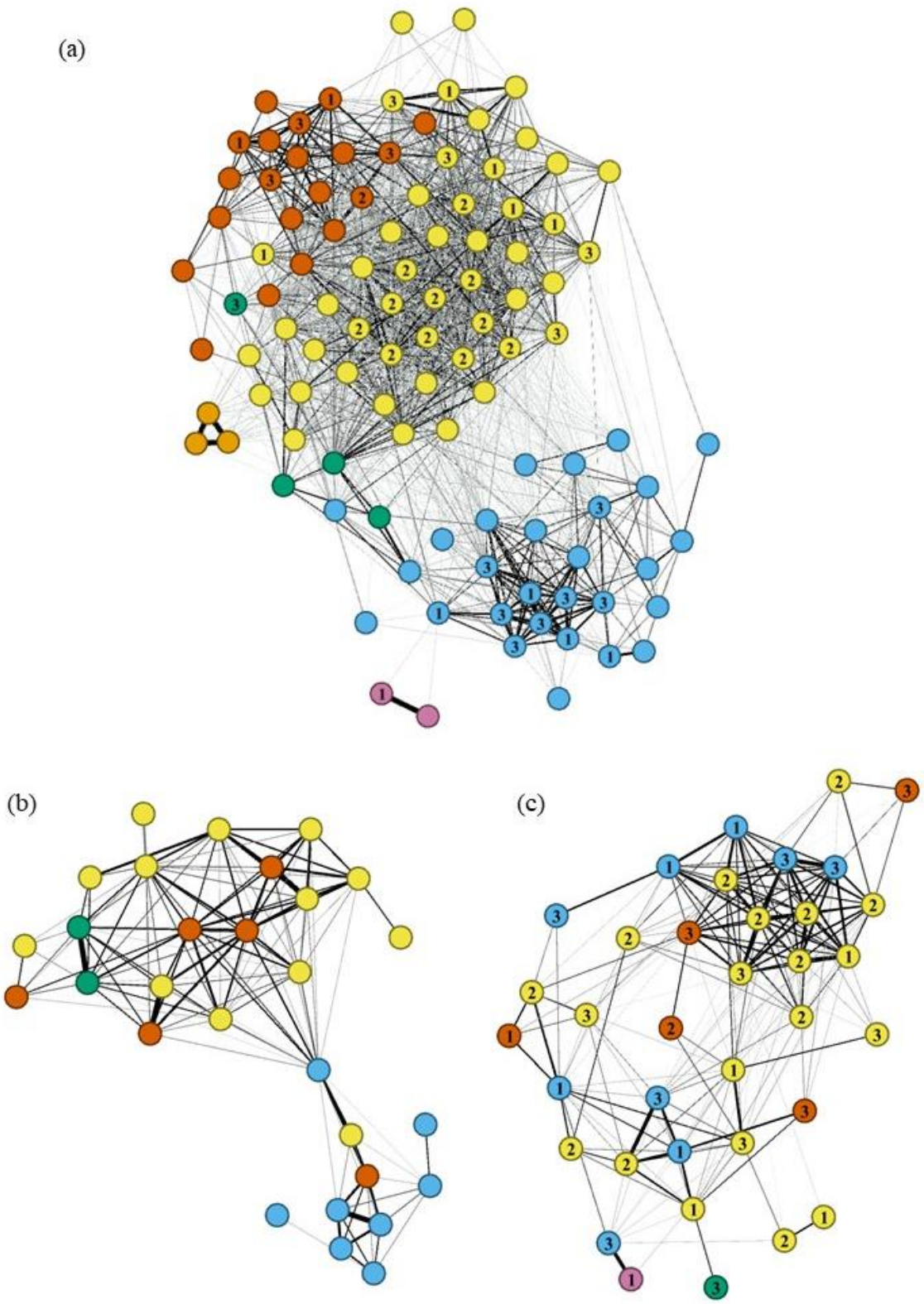



**Figure 5.2.** Hihi social networks (a) before translocation, and after translocation at (b) the source site and (c) the release site. Each node (circle) represents one hihi and the edges (lines) represents co-occurrence in a group. Edge width is proportional to association strength. Nodes in (a) are coloured by network community, and nodes in (b) and (c) are coloured by the same communities. Numbers in (a) and (c) correspond to the aviary each translocated juvenile was allocated. Networks are arranged to minimise the length of edges between nodes which tends to cluster frequently-associating nodes together.

**DID INDIVIDUALS REMAIN CONSISTENT IN THEIR SOCIALITY?**

Individual sociality was not consistent: more social juvenile hihi before translocation were not more social after the translocation at either the source site or release site (Table 5.3a, Figure 5.3a). Post-translocation social ranks did not differ between males and females (Table 5.3a) and also did not vary depending on how many times a bird was re-sighted any more than expected by random chance (Table 5.3a). Among translocated hihi, some birds experienced greater degree rank changes than others (greatest rank gain = +0.59; greatest rank loss = -0.68) but this was not predicted by their degree rank before translocation (both more- and less-sociable individuals were equally likely to change rank; Table 5.3b, Figure 5.3b). Individual degree rank was not preserved by holding a juvenile with its familiar group-mates in an aviary during the translocation (no significant difference in degree rank change between birds housed in familiar and mixed aviaries; Table 5.3b, Figure 5.3b). Finally, the extent of rank change was not significantly different between males and females (Table 5.3b), and again was not significantly affected by re-sighting before or after translocation compared to permuted networks (Table 5.3b).

**Table 5.3.** Results of (a) GLM analysing variation in post-translocation degree ranks and (b) LM analysing change in relative degree ranks for translocated hihi. Coefficients, standard errors and *z* or *t* values are presented. *P*-values generated from the original model are presented, but only for comparison to the *P*-values generated in relation to coefficients from 1000 randomised networks ($P_{rand}$). Significant *P*-values are indicated in bold font.

(a)

| | | coeff. | S.E. | *z* | *P*-value | $P_{rand}$ |
|---|---|---|---|---|---|---|
| degree rank after translocation ~ | intercept | -2.48 | 1.22 | -2.02 | **0.04** | 0.12 |
| | before translocation degree rank | 1.19 | 1.53 | 0.78 | 0.44 | 0.24 |
| | site (source site) | 2.10 | 1.35 | 1.56 | 0.12 | 0.16 |
| | sex (male) | 0.29 | 0.52 | 0.55 | 0.59 | 0.13 |
| | number of sightings after translocation | 0.18 | 0.07 | 2.59 | **0.009** | 0.27 |
| | before translocation degree rank*site (source site) | -1.67 | 1.95 | -0.86 | 0.39 | 0.17 |

(b)

| | | coeff. | S.E. | *t* | *P*-value | $P_{rand}$ |
|---|---|---|---|---|---|---|
| change in degree rank (translocated hihi) ~ | intercept | -0.05 | 0.64 | -0.07 | 0.95 | 0.95 |
| | degree rank before translocation | -0.84 | 0.80 | -1.05 | 0.30 | 0.75 |
| | aviary category (mixed) | -0.04 | 0.66 | -0.06 | 0.96 | 0.69 |
| | sex (male) | -0.05 | 0.06 | -0.90 | 0.37 | 0.22 |
| | number of sightings after translocation | 0.34 | 0.01 | 8.26 | **<0.001** | 0.23 |
| | number of sightings before translocation | 0.01 | 0.01 | 0.88 | 0.39 | 0.16 |
| | degree rank before translocation*aviary category (mixed) | 0.20 | 0.72 | 0.27 | 0.79 | 0.51 |

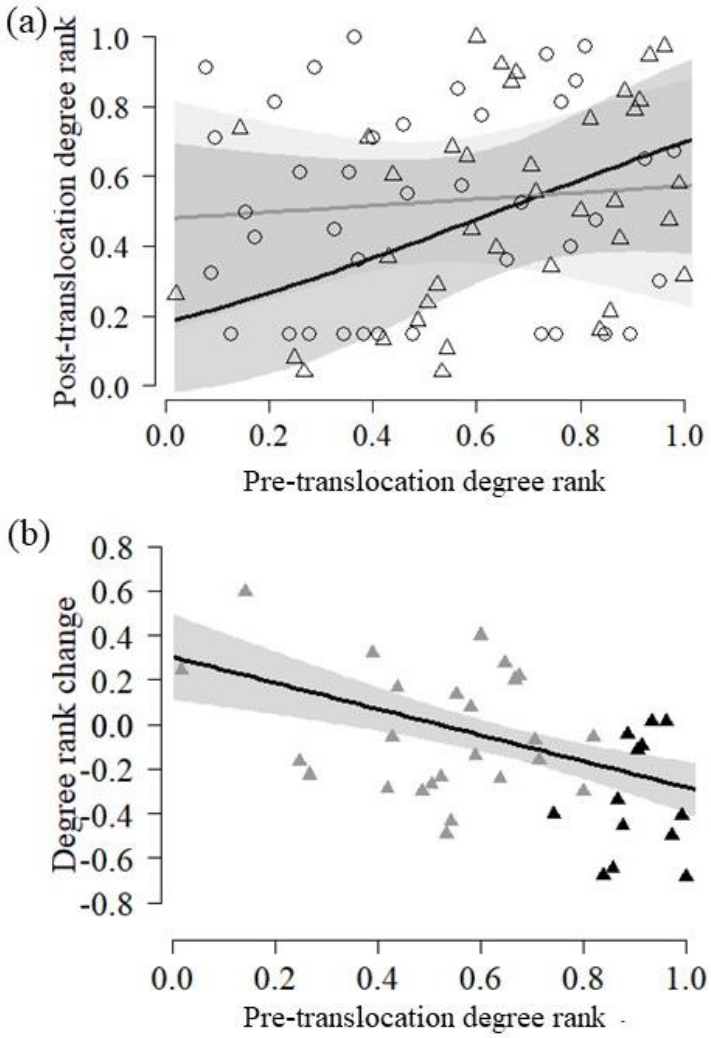



**Figure 5.3.** (a) relationship between degree ranks before and after translocation for non-translocated (circles, grey line) and translocated hihi (triangles, black line); (b) change in degree rank after compared to before translocation for translocated hihi held in mixed aviaries (grey triangles) and the familiar aviary (black triangles). Grey polygons represent 95% confidence intervals from models in Table 5.3.

**DID SOCIAL CHANGES ACROSS THE TRANSLOCATION AFFECT SURVIVAL?**

Although we could not predict rank change, among translocated hihi there was a tendency for birds that experienced a greater decline in degree rank to have poorer post-release survival: the best supported model explaining monthly survival included rank change as a covariate, and sex, while accounting for varying re-sighting between sexes (Table 5.4; Supplementary Table 5.1a). However, monthly survival was high overall (Table 5.4) so the effects of degree change and sex were weak: models with no variation in survival were included in the set with ΔQAICc < 2 (Supplementary Table 5.1a). Survival rates were not time-dependent (Supplementary Table 5.1a), so we calculated overall 11-month survival

likelihood based on monthly survival estimates from the models. 11-month survival showed greater variation, from 17.4% (95% CI = 0.2 – 66.7%) with the greatest loss of rank (-0.68) to 38.2% (95% CI = 3.0 – 78.4%) for the greatest rank gain (+0.59) (Figure 5.4). Overall male survival was 38.1% (95% CI = 12.7 – 64.6%) and female survival was 24.5% (95% CI = 3.3 – 57.5%) (Figure 5.4). For comparison, there was no evidence that degree rank change explained survival for non-translocated juveniles as it was included in models with little support (Supplementary Table 5.1b). In general, there was little support that survival varied with any predictor as many models were similarly ranked by ΔQAICc (Supplementary Table 5.1b).

**Table 5.4.** Initial model estimates of monthly post-release survival and re-sighting for translocated male and female juvenile hihi. Calculated from model averaging top-ranked models in Supplementary Table 5.1a.

| | **Survival *φ*** | | **Re-sighting *ρ*** | |
|---|---|---|---|---|
| | Effect ± SE | 95% CI | Effect ± SE | 95% CI |
| Male | 0.91 ± 0.03 | 0.80 – 0.96 | 0.94 ± 0.04 | 0.82 – 0.98 |
| Female | 0.88 ± 0.05 | 0.73 – 0.96 | 0.84 ± 0.07 | 0.67 – 0.93 |

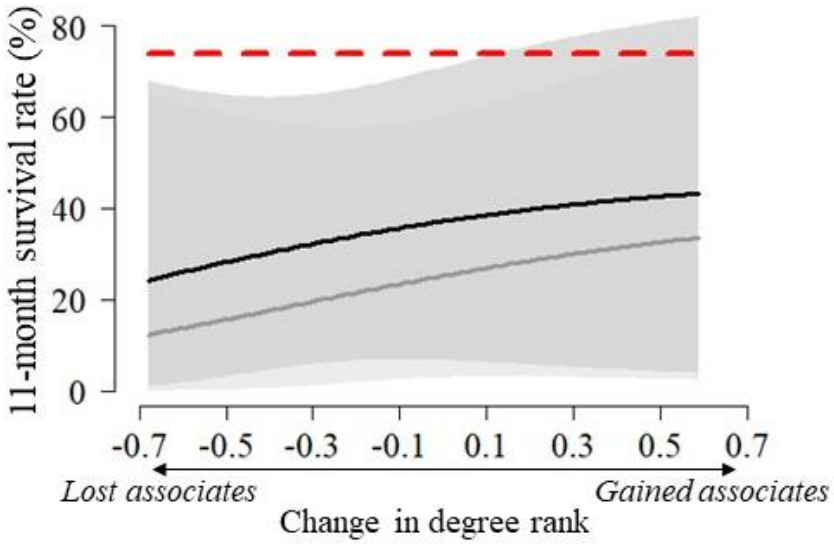



**Figure 5.4.** Predicted survival likelihood across the 11 months post-release depending on change in degree rank after translocation, for males (black line) and females (grey line). 95% confidence intervals are grey polygons. Red dashed line represents survival estimate from non-translocated birds over the same length of time and shows no variation with degree rank change. All estimates predicted from model averaging top-ranked CJS survival models in Supplementary Table 5.1.

## Discussion

Here we have shown that translocating juvenile birds affects their social structure, which in turn may influence survival during the establishment phase of a reintroduction. Hihi that remained at the source site continued to associate with others from the same communities before translocation, but juveniles translocated to a new site formed new associations at random. Furthermore, holding juveniles together in an aviary did not promote group cohesion post-release, even if they had been previously familiar; instead, there was a suggestion that translocated birds actually disassociated from aviary-mates. At the individual level, there was no evidence that hihi maintained a similar level of sociality following a translocation event if they had been more social previously, and there was no difference between males and females; the same pattern was found in non-translocated hihi as well. Maintaining a group of familiar birds in an aviary did not prevent individuals from losing associates, relative to their previous sociality. Even though we did not find what predicted loss of sociality, translocated juveniles with the greatest decrease in their relative degree ranks showed a significant reduction in survival. This meant that juvenile hihi that lost the most associates were 20% less likely to survive their first year post-release, compared to individuals that experienced the largest gain of associates. Our results suggest that translocation created a disruption to the social environment at both the group and individual level, and this may have consequences for likelihood of establishment.

Our finding that group structure changed during a reintroduction event, even when there was opportunity to maintain associations with familiar individuals (through translocating familiar hihi together), reflects results of earlier studies in other New Zealand bird species (Armstrong, 1995; Armstrong and Craig, 1995). These results were similar even though juvenile hihi are more social than the previous species studied and we also determined pre-translocation familiarity over a longer time period. Social disruption could be due to the process of translocating itself (catching, moving, and releasing) (Parker *et al.*, 2012), which maintaining groups did not overcome. Alternatively, translocation could have removed external influences on associations when animals were removed from their original source environment. Understanding how environment and animal choice drive the formation of social groups is still in its infancy (Pinter-Wollman *et al.*, 2013; Leu *et al.*, 2016), but comparing with association patterns in a group of non-translocated birds meant we are able to draw stronger conclusions to suggest why social groups may not be maintained when moved to a new site. Only when hihi were removed from their source environment during the translocation did it result in mixing of previously less associated hihi; birds that experienced social disruption (removal of associates) while remaining in the source site maintained the same group structure. This suggests environment plays a key role in structuring hihi groups. Furthermore, it may mean that such groups will never be maintained during reintroductions, which by definition involve removing animals from one environment and placing them at a new site (Ewen, Armstrong, Parker, *et al.*, 2012; IUCN/SSC, 2013).

Variation in number of associates between individuals influences a range of processes from how quickly animals find food (Aplin *et al.*, 2012) to their risk of contracting disease (Christley *et al.*, 2005). Associates may be particularly important when individuals need to rely on social information more: for example, when they have little personal information, such as following reintroduction to a new site (Kendal *et al.*, 2005; Kendal, Coolen and Laland, 2009). In feral horses (*Equus caballus*), more social foals with a higher degree score were more likely to survive the loss of members of their herds during a "catastrophic" event that removed 40% of the population (Nuñez, Adelman and Rubenstein, 2015). Importantly, pre- and post-event sociality was not consistent for each foal, and post-event sociality was especially important for survival, which suggests the current social environment conferred the strongest advantages (Nuñez, Adelman and Rubenstein, 2015). In hihi, we found similar patterns as relative pre- and post-translocation sociality did not remain consistent for both translocated individuals, and birds that remained in the source environment (but did experience social disruption through the removal of peers). In our study, however, changes in sociality only had costs for survival when additionally associated with disruption of the abiotic environment. When translocated hihi lost more associates (and experienced the biggest disruption of their social environment) they survived less well. We highlight that it may be this combination of disrupting both the social and physical environment that has the greatest consequences during the establishment phase of reintroductions. Considering that overall survival was high following this reintroduction in comparison to previous releases (for example, 19% female survival in only the first six months post-reintroduction was reported by Panfylova et al. (2016)), the impact of loss of associates may be even greater in other translocations. However, more work is needed to investigate why sociality changes; further data from translocations with lower survival may also help understand links between sociality and survival. Our release site was considered high quality for hihi (mature forest, assessed by expert members of the Hihi Recovery Group (Ewen, Adams and Renwick, 2013)) but conservation managers do not only use habitat quality to decide where to reintroduce, so future sites could be lower quality and have stronger survival pressures.

Holding animals together in temporary captivity pre-release is thought to promote group cohesion and improve the survival of translocated individuals in some species (Gusset, Slotow and Somers, 2006; Shier, 2006; Shier and Swaisgood, 2012; IUCN/SSC, 2013). However, we found the opposite direction of effect for hihi: birds kept in aviaries together showed a tendency for disassociation (suggesting avoidance) even if they had been familiar pre-capture. There was also no difference in degree rank changes between birds held in familiar and mixed groups. While all our familiar birds were ranked comparatively high for sociality, this was unlikely to be a confounder as they did not show any different trend compared to all other translocated birds. Therefore, in this species there does not appear to be a benefit of temporary captivity for maintaining or establishing a social environment. This complements previous research investigating other benefits of temporary captivity during hihi translocations. While temporary holding is a practical necessity due to the time needed to capture a required cohort, and is also used to reduce the risks of disease transmission (Ewen, Armstrong, Empson, *et al.*, 2012), there is evidence that delaying release (even by four days instead of releasing immediately) decreases hihi

post-release survival (Richardson *et al.*, 2013). The downsides of captivity for some species such as hihi question how "soft" such delayed releases are (Batson, Abbott and Richardson, 2015), and highlights that there may be a need to tailor reintroduction protocols on a species-by-species basis, while considering multiple benefits and costs of management strategies (Moseby, Hill and Lavery, 2014). Studies contrasting the effects of different treatments on conservation outcomes are essential to apply reintroduction biology effectively (Taylor *et al.*, 2017). Our use of social network analysis provided a novel and detailed way to investigate the outcomes of conservation management for both group structure and individual sociality during a reintroduction (Snijders *et al.*, 2017). By experimentally testing for changes in group structure and individual sociality during a reintroduction of hihi, our approach has provided important information for the management of this and similar species. In the case of hihi, translocation changed their group structure, which was further disrupted by holding groups in aviaries together. At the individual level, changes in associations (particularly loss of associates) was linked to mortality. Therefore, even if groups are not consistent, the quantity of associates may be important for juvenile survival during abrupt changes in the environment. Predicting this sociality change may need to be a focus of future work. Overall, we present one way that the importance of sociality can be tested, and highlight an as-yet little explored application for social network analysis to understand how social groups respond to our conservation interventions.

# CHAPTER

# 6

# General discussion

In my thesis I have explored the effects of early life social experiences on foraging behaviour in juvenile songbirds, and tested whether knowledge of social behaviour can be used to inform conservation management of hihi. When I presented young hihi with a foraging task that required learning to enable continued access to food, I found that they learned about the task differently to adult birds. However, by being social and living in groups during their first few months of independence, juveniles used peer-provided information to determine their foraging behaviour. Translocating groups of juvenile hihi to new sites lead to re-assortment of previous social connections, suggesting that translocation disrupted the social environment. This disruption may have had consequences for survival. I now discuss these results in relation to the questions I posed at the beginning of this thesis. Throughout, I also discuss directions for further research.

## *Does age affect foraging and learning?*

In Chapter 2, I showed that juvenile hihi learned about a new foraging site by exploring and exploiting patches in a different manner to adult birds. Juvenile hihi continued to sample a greater proportion of non-rewarding holes at a novel bird feeder over progressive visits, compared to adults. Juveniles also showed a lower tendency to follow a colour cue that indicated the reward. As a result, they were less likely to learn to locate a rewarding food patch (in this case, one of three holes). Similar differences in foraging have been shown between adults and juveniles in other bird species (Recher and Recher,

1969; Gochfeld and Burger, 1984; Lee, Breitwisch and Diaz, 1987; Yoerg, 1994). In some cases, juvenile foraging efficiency has been shown to improve with repeated practice (Vince, 1964). However, I found no evidence that juveniles were changing their behaviour to be more like adults as they gained more experience because age-related learning differences persisted throughout my entire two-week experiment. Juveniles may take several months to reach the same level of foraging skills as adults (Goss-Custard and Durell, 1987; Yoerg, 1994) so the duration of the experiment may have been too short for young hihi to change their learning strategies.

I suggested two explanations for the age-related differences in foraging behaviour. First, continuing to test different foraging patches could be an adaptive strategy for juveniles that maintains an up-to-date picture of the current foraging landscape. Thus, juvenile hihi will have recent information on alternative locations to forage, should the environment change and their current options become depleted (Krebs, Kacelnik and Taylor, 1978; Dall *et al.*, 2005) or if they are displaced by competitive interactions with more dominant individuals (Sol *et al.*, 1998). Alternatively, juvenile inexperience (Galef and Laland, 2005) may mean they require more extensive trial-and-error learning than adults to shape the appropriate behavioural response. This is because areas of the brain that are required for processing information when modifying behaviour have not yet matured fully (Marchetti and Price, 1989). Whether age-related differences in learning were a flexible sampling strategy or an effect of inexperience, there are costs associated with juvenile foraging behaviour. In Chapter 2 I also showed young hihi had to forage for longer to obtain the same intake as adult birds. If information cannot be used correctly to reduce uncertainty (Dall *et al.*, 2005), more extensive trial-and-error will result in slower learning that wastes more energy. However, there may also be costs from sampling, if continuing to visit non-rewarding foraging patches means that optimal intake is not maintained (Krebs, Kacelnik and Taylor, 1978). Flexible behaviour (such as sampling) can be associated with lower survival, highlighting that this strategy is not always beneficial (Madden *et al.*, 2018). Although the costs associated with all behavioural challenges I used during my PhD were small (necessary because hihi are a threatened species and we cannot compromise their survival), if juveniles remain less effective at foraging in more challenging natural environments, then we may see greater impacts of missed feeding opportunities on survival. This provides a potential explanation for why many recently-independent juvenile birds are more susceptible to starvation than adults (Weathers and Sullivan, 1991; Naef-Daenzer and Grüebler, 2016).

Overall, Chapter 2 set the scene for *why* young hihi may benefit from social information use (Figure 6.1). In the context of trade-offs between social and personal information acquisition to inform learning, if juveniles are sampling to maintain patch knowledge, using socially-provided information about different food resources reduces the costs associated with prolonged sampling to help them forage optimally (Templeton and Giraldeau, 1996). Alternatively, if trial-and-error learning takes longer to acquire new skills, then social information will be favoured to help reduce the need for such learning (Kendal *et al.*, 2005). I next tested what opportunities there are for juvenile hihi to use social information.

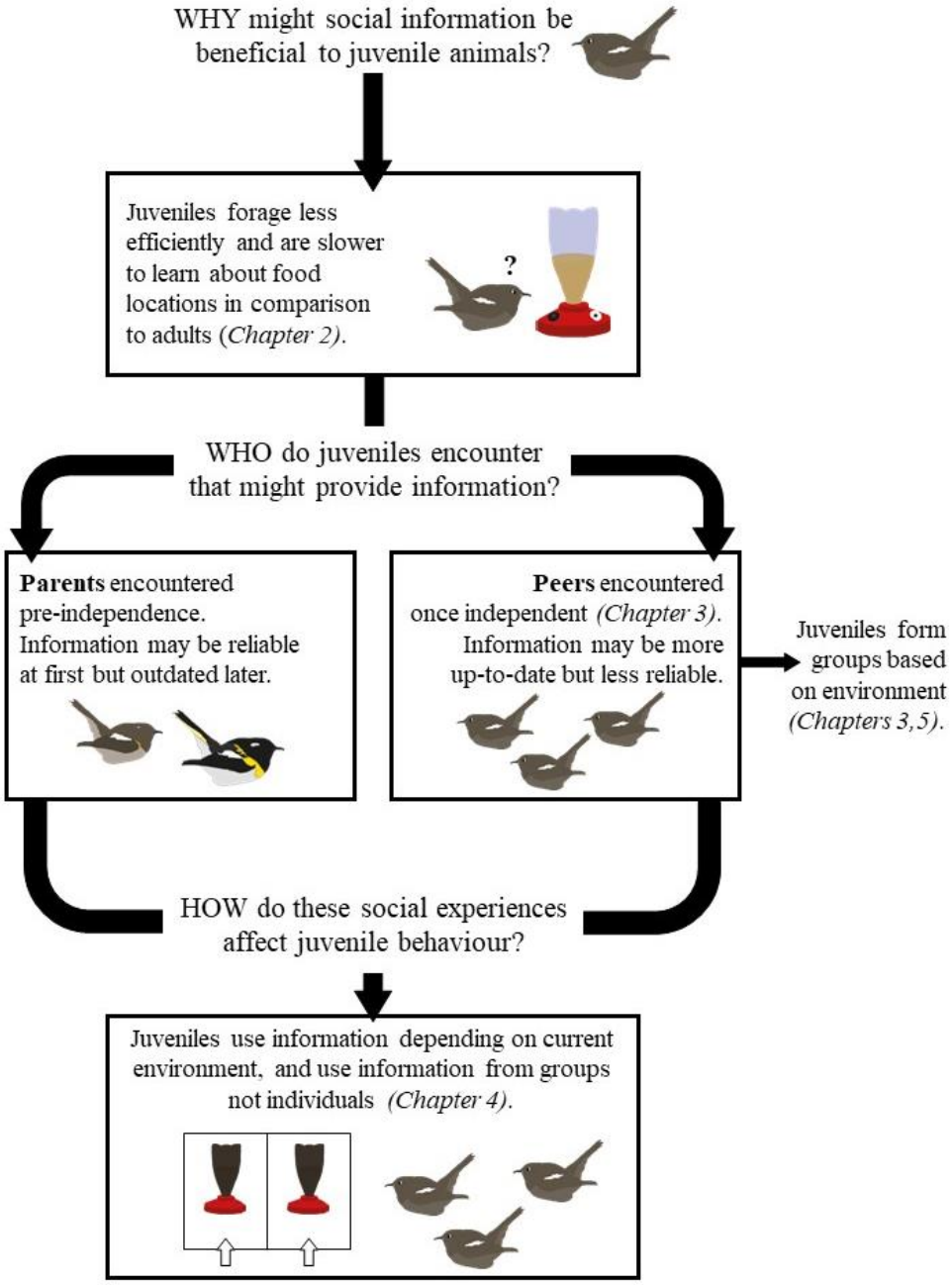



**Figure 6.1.** Summary of the importance of early life social experiences for juvenile behaviour based on evidence collected throughout this thesis. This demonstrates why juveniles need to use social information, who they encounter to provide it, and how they appear to flexibly inform behaviour in groups depending on the current environment.

## *Why do juveniles form groups?*

Juvenile hihi in my main study population (Tiritiri Matangi Island) form groups across late summer and autumn during the first few months of their post-fledge life. In Chapter 3, I provided evidence from three successive breeding seasons to show that these groups are centred around particular locations and are dominated by juveniles. Adults were not present in groups to the same extent, so there was relatively little opportunity to interact with more experienced individuals versus other juveniles. Some, but not all, juveniles moved between the spatially-separated groups, and associations developed between individuals that were frequently present in the same group sites. Thus, hihi groups resemble juvenile "gangs" (Ward and Zahavi, 2008; Dall and Wright, 2009). I also observed interactions between juveniles in groups, most frequently "huddling" (lining up together on a branch); although these behaviours suggested that birds could be developing associations through direct interactions with each other, largely they did not predict the number of network associates (degree).

In Chapter 3 I discussed how it can be difficult to determine the direction of causality between environment and social network structure (Pinter-Wollman *et al.*, 2013; Snijders *et al.*, 2017): that is, did associating hihi visit the same locations together (Firth and Sheldon, 2016) or were hihi attracted to a location which then led to associations (Leu *et al.*, 2016)? Removing a group of birds from their environment during the reintroduction in Chapter 5 and comparing their social network patterns to birds that were not moved (Snijders *et al.*, 2017), provided more evidence to understand the drivers of associations. Juvenile hihi formed new associations once they were moved to a new site, which suggested that their interactions primarily resulted from environment use. Furthermore, there were relatively consistent patterns in groups year-to-year in Chapter 3, even when individuals differed between each cohort of juveniles; this could be because groups may have been determined by particular environmental factors such as availability of limited water resources across the three years. While my PhD focused on the social structure and effect of such groups and not the exact reasons that juveniles were visiting these locations, similar juvenile groups in other species like raven (*Corvus corax*) (Dall and Wright, 2009) or quelea (*Quelea quelea*) (Ward and Zahavi, 2008) respond to ephemeral food resources while operating around stable social meeting places (for example, roosts). Thus, resources such as food, water and roost sites may well also be important to juvenile hihi social groups.

Understanding the characteristics of individuals in groups in Chapter 3 provided an invaluable basis that I then used to understand the outcomes of social behaviour in Chapter 4 (Farine, Montiglio and Spiegel, 2015). The comparatively greater presence of other juveniles rather than adult hihi in groups suggested that "horizontal" information transmission opportunities could be common, compared to few "vertical" (from parents) or "oblique" opportunities (van Schaik, 2010). Groups could therefore also act as "information centres" to inform foraging, if they perform in a similar way to juvenile-dominated groups in

other bird species which allow for social learning from peers (i.e. quelea and ravens: Ward and Zahavi, 2008; Dall and Wright, 2009). In Chapter 4, I demonstrated that the horizontally-provided information from collective behaviour of these groups influenced individual foraging behaviour. Juvenile hihi were more likely to choose one of two foraging choices when more of their peers also visited that same choice. Furthermore, their response to their peers meant they appeared to use current information provided from other individuals in the same time and place to inform foraging, rather than retaining behaviours learned earlier with parents. In some species, behaviours learned early in life can last a lifetime (Slagsvold and Wiebe, 2011). These behaviours can arise from one-to-one interactions (for example, shown in banded mongoose *Mungos mungo,* although they may also learn from helpers not directly related to the juvenile) (Sheppard *et al.*, 2018). However, other species do not maintain the exact details of early-learned behaviours (Fox and Millam, 2004), and juvenile hihi reflect this latter strategy. By copying their peers, instead of retaining information from parents, this may allow behaviour to change more flexibly depending on social environments encountered later in life. More generally, the use of social information provided by a group is a widespread strategy generally thought to help animals overcome their own uncertainties and assess the quality of feeding patches, mates, or competitors (Valone and Templeton, 2002; Danchin *et al.*, 2004). Further, using information gathered from many peers in groups can avoid the potential costs of using social information because animals can determine what to copy based on the relative uses of alternative behaviours (King and Cowlishaw, 2007). As an extension, therefore, I suggest group-provided information may be particularly valuable for naïve individuals such as juveniles during a period of their lives when survival is challenging.

The behaviour of groups was copied to the extent that across my Chapter 4 experiment, a socially-facilitated preference developed among juveniles. As a result, individuals converged on one of the two feeder side choices, which was actually the opposite side between two spatially-separated feeder sites. As yet, this is one of the few studies that provides evidence for conformity effects (*sensu*: de Waal, 2013) on foraging behaviour in wild birds (Aplin *et al.*, 2015). Although there is value to copying groups of peers, one consideration is that using social information to the extent that leads to conformity may mean that animals do not fully exploit the environment. Why animals copy others to such an extent is still the subject of discussion (Aplin, Sheldon and McElreath, 2017). For example, during my experiment in Chapter 4, the opposite (equally rewarding) side of the feeder became less used. This could be viewed as a maladaptive outcome of conforming, as it meant that hihi did not fully exploit the environment. However, there are several reasons why copying the majority was not necessarily a poor strategy in this case. Firstly, as part of my experimental design the food resource in the feeder never ran out; therefore, hihi never had to adjust foraging to respond to a depleted food patch, as would need to occur when foraging more naturally (Pyke, 1978). Further, I also demonstrated hihi may actually show some adjustment of behaviour depending on payoff, suggesting copying is flexible: in Chapter 4, hihi were less likely to choose the same side when visiting very closely together. Thus, even while juveniles appear to rely on social information to inform foraging for the most part, under particular conditions they can also use their own experiences to avoid competition, which is one of inherent costs associated with group living (Rubenstein, 1978). Potentially, this is when continued sampling of the environment (one

explanation for the learning patterns seen in Chapter 2) could become important, if it maintains up-to-date information about alternative foraging options. However, more studies of conformity under varying pay-off (Aplin, Sheldon and McElreath, 2017) are required to help understand whether groups that are seemingly reliant on peer-provided information, such as those formed by juveniles, do use social learning adaptively.

If the behaviour of groups of peers as a whole is important, the relationships between any specific individuals may be less crucial. Although competition or aggression can increase between unfamiliar individuals (Eason and Hannon, 1994; Chuang, Kam and Bee, 2017), associating randomly (with both familiar and unfamiliar individuals) provides information from peers with a range of different experiences (the "any social partners" hypothesis from Ramakers et al. (2016)). This theory may explain why the choices of specific individuals, the preceding bird visiting my experimental feeders in groups, were less important in Chapter 4. This was despite evidence for different strengths of associations in Chapter 3 (which remain to be explained). More familiar hihi also did not forage together later in life (based on evidence from a minor extra study I conducted, see Appendix 3). Finally, the benefits of groups containing a mix of peers could also explain why previous associations were not maintained following the reintroduction in Chapter 5, as social information from novel peers could buffer limited knowledge in a new site (Kendal *et al.*, 2005; Rendell *et al.*, 2010). Alternatively, one consideration is that recognising and tracking individuals is more cognitively demanding (Aplin *et al.*, 2015a), so it is possible hihi may not possess this ability. However, while my results showed that familiarity did not affect social information use, more generally some animals do prefer to associate with and learn from more familiar peers (Schwab *et al.*, 2008), especially when inexperienced or uncertain (Pinter-Wollman, Isbell and Hart, 2009). Conversely, others choose unaffiliated individuals (Schwab, Bugnyar and Kotrschal, 2008; Ramakers *et al.*, 2016). Thus, more work is needed to understand the effect of different contexts on the importance of familiarity.

Chapters 3 and 4 demonstrated *who* provides social information to young hihi, and *how* they use such information to adjust foraging behaviour and potentially offset their inexperience (Figure 6.1). As such it showed that juvenile hihi are social and live in groups with peers during their first few months of independence from parents. Information provided by these groups influences their foraging behaviour in a way that appears to buffer any one individual's naivety. However, juveniles may also need to adjust their extent of social information use at times when this strategy becomes less adaptive; the amount that they do so requires more investigation to further our understanding of the benefits and costs of group living for young animals.

## What are the benefits of social groups for conservation?

Animals change behaviour as a first step to adapt to altered environments (Wong and Candolin, 2014), so understanding how social experiences inform their learning is crucial for predicting their behavioural responses during conservation interventions such as reintroductions (Blanchet, Clobert and Danchin, 2010). Evidence from Chapters 2, 3, and 4 gave me an understanding of the importance of group social experiences for informing foraging behaviour in juvenile hihi. This provided insight into the potential implications of social groups for conservation practices involving these young animals (Sutherland, 1998; Blumstein, 2010). Therefore, in Chapter 5 I tested whether knowledge of groups could inform management of the social environment during a reintroduction, and whether this might predict survival during establishment.

A recent review highlighted the potential applications of social network theory to conservation (Snijders *et al.*, 2017), because it can help track changes in animal social systems in response to environmental changes created by humans, and highlight likely impacts of such changes on population stability. In Chapter 5 I used network analysis to explore if juvenile hihi maintained social groups during one form of conservation intervention (a reintroduction), particularly if kept together with group-mates. I showed that juvenile hihi formed new associations once released at a new site, and groups created during a period of temporary captivity did not promote social group cohesion even if the birds had been familiar pre-reintroduction. Instead, there was a minor tendency for hihi to disassociate from others that had been in the same aviary. Thus, while familiarity may not be important in most contexts, the identity of social partners might start to become important in some situations (leading to either stronger associations, or avoidance). Potentially, disassociation could arise if temporary captivity is stressful and causes animals to avoid one another (Farine, Spencer and Boogert, 2015). However, we would need to test for changes in stress levels (for example, corticosterone concentrations (Batson *et al.*, 2017)) to understand whether they may explain associations post-release.

Further, using network analysis helped to understand the consequences of temporary captivity on social groups, which is crucial to inform effective use of delayed release (IUCN/SSC, 2013; Batson, Abbott and Richardson, 2015). Despite being viewed as a beneficial strategy to acclimate groups to release sites or promote group cohesion, there is increasing evidence that delaying releases can decrease post-release survival (hihi: Richardson et al., 2013; other species: Batson et al., 2015; Moseby et al., 2014). Further, consequences vary between species (Moseby, Hill and Lavery, 2014), highlighting the need for investigation of species-level responses to reintroduction management to understand the benefits. There could also be longer term effects of social disruption from translocation and temporary captivity, as changes in social groups might impact on later mate choice in the new site (Driscoll, 2007). These different levels of disruption may need to be integrated (for example, through modelling) to translate evidence of different outcomes from management into effective conservation practice.

Along with group-level change, there was also some evidence that changes in number of associates may be important when individuals experience abrupt disruption of social groups. Relative sociality (compared to other juveniles) did not remain consistent following the reintroduction in either the non-translocated or translocated juveniles. Similar findings from previous studies have shown that individual-level sociality changes following disruption (Nuñez, Adelman and Rubenstein, 2015; Firth *et al.*, 2017). However, only in translocated hihi was there a link between larger loss of sociality and a tendency to survive less well, suggesting that a combination of social and environmental disruption was detrimental. Therefore, if an individual has had the chance to associate with many others but then abruptly losing these associates while also being moved to a new site, this could be when imposed changes in sociality are important (Nuñez, Adelman and Rubenstein, 2015). More work is needed to understand the effects of such changes following this initial investigation, especially as I only found weak differences in survival; this may include replicating over repeated reintroductions as a valuable way to test further if the combination of extensive abiotic (environment) and biotic (social) disruption leads to lowered survival. A further step could also be to explore broader consequences of such changes on group behaviour (for example, how groups locate food resources post-reintroduction and whether number of associates is important for foraging, see Appendix 3) (Firth, Sheldon and Farine, 2016). This would help better understand why survival may be affected by changes in sociality.

Results throughout my chapters suggested other potential ways that social groups could be important to reintroductions, which were not directly tested but remain worthwhile to consider. When animals update their behaviour using information from current associates, and do not maintain responses from previous experiences (Chapter 4) this may have implications for reintroduction programmes that aim to elicit particular behavioural responses in their translocated cohort. For example, pre-release training (by humans or conspecifics) can allow young animals to learn to avoid predators (Shier and Owings, 2007; Alonso *et al.*, 2011) or forage better on their natural food sources after captive rearing (Whiteside, Sage and Madden, 2015). Training can increase survival chances once the animals are released (Shier and Owings, 2007; Alonso *et al.*, 2011; Whiteside, Sage and Madden, 2015). However, if juveniles change behaviours in response to peer-provided information then there may be less value to training pre-reintroduction. In a study by Teitelbaum, Converse, & Mueller (2018), whooping cranes (*Grus americana*) trained to migrate using two different methods (conspecifics and aircraft) later converged in migration behaviour. Aircraft-trained birds adopted the migration patterns of conspecific-trained birds, which meant that the implemented changes in migration sites were not maintained. In such cases, periodic re-training may be required to maintain behaviours in reintroductions; by understanding how and when social experiences affect behaviour, managers can decide when it is best to implement interventions (Teitelbaum, Converse and Mueller, 2018).

When animals benefit from the presence of conspecifics, this is broadly known as an “Allee effect” (Stephens and Sutherland, 1999). Allee effects from group size have been suggested to be important for conservation behaviour because of their influence on mating systems (determining conspecific attraction), and dispersal (source and sink dynamics) (Stephens and Sutherland, 1999; Courchamp,

Berec and Gascoigne, 2008). When groups become smaller, Allee effects weaken: for example, small groups limit foraging efficiency because animals cannot use the successes of conspecifics to inform their own behaviour (Courchamp, Berec and Gascoigne, 2008). This may be because the prevalence of alternative behaviours can fluctuate more easily in small populations, leading less reliable collective group information (King and Cowlishaw, 2007). Further, shifts in group-level behaviour may mean small groups also become more susceptible to "social tipping points" (drastic changes in behaviour) (Pruitt *et al.*, in press). Potentially, the limited evidence for social effects in the smaller population used for my initial study in Chapter 2 might have been due to group sizes: although juveniles were of a similar age to my main study population (the breeding season at Zealandia is c. 2 months behind Tiritiri Matangi) the small groups at Zealandia (maximum number of individuals seen at once = 4) could have limited social learning. This would need to be tested in more detail to provide stronger evidence for effects of varying group size on social learning, but would also help to assess further the apparent value of social groups to learning by naïve juveniles. For reintroductions in species where there are apparent Allee effects, group size may be particularly important during establishment if animals rely on socially-provided information from groups to overcome uncertainty (Kendal *et al.*, 2005; Rendell *et al.*, 2010).

In summary, my thesis has provided evidence to understand why young, inexperienced wild animals may benefit from using socially-provided information when foraging, what information they encounter during early-life experiences, and how they use such information to inform foraging decisions. As such, it has provided a comprehensive overview of behaviour during early life in hihi, which is rarely available from wild birds. Furthermore, I have also tested the importance of managing social groups for conservation of a threatened species, and found that abrupt losses in associates during translocations to new sites may negatively impact on survival. Together, my results therefore suggest that social experiences in groups provide information that juvenile animals can use to buffer their own inexperience, and the presence (but not always identity) of conspecifics may be particularly important when adjusting to changing natural environments.

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# APPENDIX 1: SUPPLEMENTARY MATERIAL

Supplementary tables and figures in this Appendix are numbered according to their corresponding Chapter. Tables appear before figures in each section.

## *A1.1. Chapter 2 supplementary tables*

**Supplementary Table 2.1.** Ranking of all generalised linear mixed effects models used to analyse (a) variation in first hole attempted, and (b) variation in all holes attempted, and (c) proportion of non-rewarding holes attempted out of total number holes. Predictors include trial number, age (adult vs. juvenile), learning sequence (1 or 2), and social category (alone, semi-social, social). Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. All models contained a random effect term to account for repeated trials by individuals (trial number | ID). Null models (~1) are presented for comparison.

(a)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ trial number + age | 392.64 | 0.00 | 0.43 |
| ~ trial number*age + learning sequence | 395.19 | 2.55 | 0.12 |
| ~ trial number + age + learning sequence | 395.24 | 2.60 | 0.12 |
| ~ trial number | 395.53 | 2.89 | 0.10 |
| ~ trial number*learning sequence + age | 396.12 | 3.48 | 0.08 |
| ~ trial number + age + social category | 397.90 | 5.26 | 0.03 |
| ~ trial number + learning sequence*age | 397.94 | 5.30 | 0.03 |
| ~ trial number*age + social category | 398.01 | 5.36 | 0.03 |
| ~ trial number + learning sequence | 398.03 | 5.39 | 0.03 |
| ~ trial number + social category | 400.52 | 7.88 | 0.01 |
| ~ trial number + age + learning sequence + social category | 400.72 | 8.08 | 0.01 |
| ~ trial number*age + learning sequence + social category | 400.89 | 8.25 | 0.01 |
| ~ trial number*learning sequence + age + social category | 401.89 | 9.25 | 0.00 |
| ~ trial number + learning sequence + social category | 403.23 | 10.59 | 0.00 |
| ~ trial number + learning sequence*age + social category | 403.66 | 11/02 | 0.00 |
| ~ trial number*learning sequence + social category | 404.41 | 11.77 | 0.00 |
| ~ age | 428.88 | 36.24 | 0.00 |

| | | | |
|---|---|---|---|
| ~ colour of first hole attempted | 430.05 | 37.41 | 0.00 |
| ~ age + learning sequence | 431.25 | 38.61 | 0.00 |
| ~ age + social category | 433.68 | 41.04 | 0.00 |
| ~ 1 | 434.55 | 41.91 | 0.00 |
| ~ learning sequence + age + social category | 436.23 | 43.59 | 0.00 |
| ~ learning sequence | 436.87 | 44.23 | 0.00 |
| ~ learning sequence*age + social category | 438.50 | 45.86 | 0.00 |
| ~ social category | 439.21 | 46.57 | 0.00 |
| ~ learning sequence + social category | 441.71 | 49.07 | 0.00 |

(b)

| | **AICc** | **∆AICc** | **AICc Weight** |
|---|---|---|---|
| ~ trial number | 1195.57 | 0.00 | 0.30 |
| ~ trial number + age + learning sequence | 1195.71 | 0.14 | 0.28 |
| ~ trial number + age*learning sequence | 1196.72 | 1.16 | 0.17 |
| ~ trial number*learning sequence + age | 1198.38 | 2.81 | 0.07 |
| ~ trial number*age + learning sequence | 1198.42 | 2.85 | 0.07 |
| ~ trial number + age + social category | 1200.10 | 4.53 | 0.03 |
| ~ trial number + learning sequence + social category | 1200.92 | 5.36 | 0.02 |
| ~ trial number + age + learning sequence + social category | 1201.21 | 5.65 | 0.02 |
| ~ trial number + age*learning sequence + social category | 1202.41 | 6.85 | 0.01 |
| ~ trial number*age + social category | 1202.85 | 7.28 | 0.01 |
| ~ trial number*learning sequence + social category | 1203.75 | 8.19 | 0.01 |
| ~ trial number*learning sequence + age + social category | 1204.12 | 8.55 | 0.00 |
| ~ trial number*age + learning sequence + social category | 1204.16 | 8.60 | 0.00 |
| ~ age | 1209.74 | 14.17 | 0.00 |
| ~ learning sequence + age | 1211.36 | 15.79 | 0.00 |
| ~ 1 | 1214.23 | 18.67 | 0.00 |
| ~ learning sequence | 1214.76 | 19.19 | 0.00 |
| ~ colour of first hole attempted | 1216.51 | 20.94 | 0.00 |
| ~ social category | 1218.68 | 23.12 | 0.00 |
| ~ learning sequence + social category | 1219.69 | 24.13 | 0.00 |

(c)

| | **AICc** | **∆AICc** | **AICc Weight** |
|---|---|---|---|
| ~ trial number*learning sequence + age | 446.04 | 0.00 | 0.65 |
| ~ trial number*age + learning sequence | 449.33 | 3.29 | 0.12 |
| ~ trial number + learning sequence + age | 449.90 | 3.86 | 0.09 |
| ~ trial number | 451.56 | 5.52 | 0.04 |

| | | | |
|---|---|---|---|
| ~ trial number + age*learning sequence | 452.47 | 6.43 | 0.03 |
| ~ trial number*age + social category | 453.13 | 7.10 | 0.02 |
| ~ trial number + age + social category | 453.67 | 7.64 | 0.01 |
| ~ trial number*learning sequence + age + social category | 454.10 | 8.06 | 0.01 |
| ~ trial number + age*learning sequence + social category | 454.93 | 8.89 | 0.01 |
| ~ trial number*age+ learning sequence + social category | 454.96 | 8.92 | 0.01 |
| ~ trial number + age + learning sequence + social category | 455.07 | 9.03 | 0.01 |
| ~ trial number + learning sequence + social category | 457.62 | 11.58 | 0.00 |
| ~ trial number*learning sequence + social category | 458.81 | 12.78 | 0.00 |
| ~ age | 479.50 | 33.46 | 0.00 |
| ~ learning sequence + age | 481.30 | 35.26 | 0.00 |
| ~ 1 | 485.55 | 39.51 | 0.00 |
| ~ colour of first hole visited | 485.77 | 39.74 | 0.00 |
| ~ learning sequence | 486.88 | 40.84 | 0.00 |
| ~ social category | 490.40 | 44.36 | 0.00 |
| ~ learning sequence + social category | 491.97 | 45.93 | 0.00 |

**Supplementary Table 2.2.** Ranking of generalised linear mixed effects models used to analyse how (a) proportion of time spent at the reward hole while in the feeding arena, and (b) total time spent in the feeding arena, varied with age as a predictor variable. Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. All models contained a random effect term to account for repeated records of individuals (1 | ID). Null models (~1) are presented for comparison.

(a)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ 1 | 234.75 | 0.00 | 0.60 |
| ~ age | 235.59 | 0.84 | 0.40 |

(b)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ age | 6773.97 | 0.00 | 0.85 |
| ~ 1 | 6777.40 | 3.43 | 0.15 |

**Supplementary Table 2.3.** Ranking of generalised linear mixed effects models used to analyse (a) effect of inter-trial interval on likelihood of visiting reward hole first, and (b) effect of inter-trial interval on variation in number of wrong holes visited on return to the feeder arena, and (c) variation in inter-trial interval with age. For (a) and (b) predictors include inter-trial interval (log-transformed seconds to account for large variation in scale compared to other predictors), and age (adult vs. juvenile). For (c), predictors include age only. All models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. All models contained a random effect term to account for repeated trials by individuals (1|ID). Null models (~1) presented for comparison.

(a)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ inter-trial interval + age | 285.73 | 0.00 | 0.37 |
| ~ inter-trial interval*age | 285.84 | 0.11 | 0.35 |
| ~ inter-trial interval | 286.33 | 0.60 | 0.28 |
| ~ age | 388.87 | 103.14 | 0.00 |
| ~ 1 | 393.45 | 107.72 | 0.00 |

(b)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ inter-trial interval *age | 437.02 | 0.00 | 0.99 |
| ~ inter-trial interval + age | 446.09 | 9.07 | 0.01 |
| ~ inter-trial interval | 449.41 | 12.39 | 0.00 |
| ~ age | 621.21 | 184.19 | 0.00 |
| ~ 1 | 630.58 | 193.56 | 0.00 |

(c)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ age | 1787.95 | 0.00 | 0.76 |
| ~ 1 | 1790.22 | 2.27 | 0.24 |

## *A1.2. Chapter 3 supplementary tables and figures*

**Supplementary Table 3.1.** Multistate models ranked by ΔQAICc values analysing re-sighting (*ρ*) and movement (*Ψ*) between groups of adult and juvenile hihi for (a) 2015, (b) 2016, and (c) 2017, depending on age of individuals, time (recapture event) and group sites. Null model *S*(.) *ρ*(.) *Ψ*(.) included for comparison. All models corrected by median ĉ following goodness-of-fit testing. AICc weight indicates relative likelihood of each model.

(a)

| | QAICc | ΔQAICc | AICc Weights | Number of parameters |
|---|---|---|---|---|
| S(.)ρ(age)ψ(age+site) | 232.40 | 0.00 | 0.35 | 5 |
| S(.)ρ(age)ψ(age) | 232.70 | 0.29 | 0.30 | 4 |
| S(.)ρ(age)ψ(.) | 234.08 | 1.68 | 0.15 | 4 |
| S(.)ρ(age)ψ(site) | 234.20 | 1.79 | 0.14 | 5 |
| S(.)ρ(age+time)ψ(age+site) | 238.55 | 6.15 | 0.02 | 11 |
| S(.)ρ(age+time)ψ(age) | 238.62 | 6.22 | 0.02 | 10 |
| S(.)ρ(age+time)ψ(.) | 240.01 | 7.61 | 0.01 | 10 |
| S(.)ρ(age+time)ψ(site) | 240.35 | 7.94 | 0.01 | 11 |
| S(.)ρ(.)ψ(age+site) | 240.73 | 8.32 | 0.01 | 4 |
| S(.)ρ(.)ψ(.) | 242.44 | 10.04 | 0.00 | 3 |
| S(.)ρ(time)ψ(site+age) | 247.01 | 14.61 | 0.00 | 10 |
| S(.)ρ(time)ψ(age) | 247.12 | 14.72 | 0.00 | 9 |
| S(.)ρ(age*time)ψ(age) | 247.33 | 14.92 | 0.00 | 16 |
| S(.)ρ(age*time)ψ(age+sites) | 247.52 | 15.11 | 0.00 | 17 |
| S(.)ρ(time)ψ(.) | 248.51 | 16.10 | 0.00 | 9 |
| S(.)ρ(age*time)ψ(.) | 248.71 | 16.31 | 0.00 | 16 |
| S(.)ρ(time)ψ(site) | 248.81 | 16.40 | 0.00 | 10 |
| S(.)ρ(age*time)ψ(sites) | 249.31 | 16.91 | 0.00 | 17 |

(b)

| | QAICc | ΔQAICc | AICc Weights | Number of parameters |
|---|---|---|---|---|
| S(.)ρ(age+time)ψ(age+sites) | 869.66 | 0.00 | 0.88 | 21 |
| S(.)ρ(age+time)ψ(sites) | 874.32 | 4.66 | 0.09 | 20 |
| S(.)ρ(age+time)ψ(age) | 876.37 | 6.71 | 0.03 | 17 |
| S(.)ρ(age+time)ψ(.) | 881.03 | 11.37 | 0.00 | 16 |
| S(.)ρ(time)ψ(age+sites) | 884.84 | 15.19 | 0.00 | 20 |
| S(.)ρ(time)ψ(sites) | 889.52 | 19.86 | 0.00 | 19 |
| S(.)ρ(age*time)ψ(age+sites) | 890.28 | 20.62 | 0.00 | 33 |

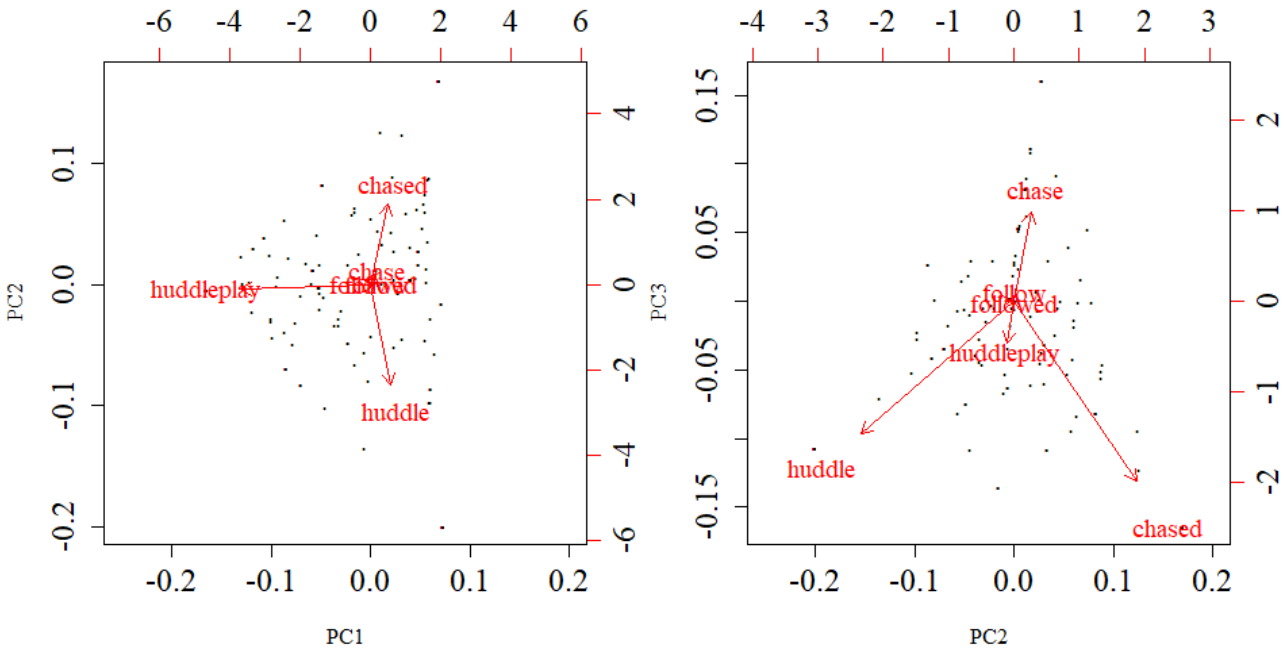
| | | | | |
|---|---|---|---|---|
| S(.)ρ(age)ψ(age+sites) | 891.09 | 21.43 | 0.00 | 9 |
| S(.)ρ(time)ψ(age) | 891.62 | 21.96 | 0.00 | 16 |
| S(.)ρ(age*time)ψ(sites) | 894.74 | 25.08 | 0.00 | 32 |
| S(.)ρ(age)ψ(sites) | 895.93 | 26.27 | 0.00 | 8 |
| S(.)ρ(age*time)ψ(age) | 896.19 | 26.53 | 0.00 | 29 |
| S(.)ρ(time)ψ(.) | 896.29 | 26.63 | 0.00 | 15 |
| S(.)ρ(age)ψ(age) | 898.51 | 28.85 | 0.00 | 5 |
| S(.)ρ(.)ψ(age+sites) | 903.28 | 33.62 | 0.00 | 8 |
| S(.)ρ(age)ψ(.) | 903.34 | 33.68 | 0.00 | 4 |
| S(.)ρ(.)ψ(.) | 915.60 | 45.95 | 0.00 | 3 |

(c)

| | **QAICc** | **ΔQAICc** | **AICc Weights** | **Number of parameters** |
|---|---|---|---|---|
| S(.)ρ(age)ψ(age+sites) | 1434.21 | 0.00 | 0.99 | 10 |
| S(.)ρ(age)ψ(sites) | 1443.48 | 9.26 | 0.01 | 9 |
| S(.)ρ(age+time)ψ(age+sites) | 1447.63 | 13.41 | 0.00 | 28 |
| S(.)ρ(age)ψ(age) | 1456.37 | 22.16 | 0.00 | 5 |
| S(.)ρ(age+time)ψ(sites) | 1456.76 | 22.55 | 0.00 | 27 |
| S(.)ρ(age)ψ(.) | 1463.00 | 28.79 | 0.00 | 4 |
| S(.)ρ(.)ψ(age+sites) | 1463.69 | 29.48 | 0.00 | 9 |
| S(.)ρ(age+time)ψ(age) | 1469.17 | 34.96 | 0.00 | 23 |
| S(.)ρ(age*time)ψ(age+sites) | 1472.60 | 38.38 | 0.00 | 46 |
| S(.)ρ(age+time)ψ(.) | 1475.68 | 41.47 | 0.00 | 22 |
| S(.)ρ(time)ψ(age+sites) | 1477.41 | 43.20 | 0.00 | 27 |
| S(.)ρ(age*time)ψ(sites) | 1481.60 | 47.39 | 0.00 | 45 |
| S(.)ρ(time)ψ(sites) | 1486.56 | 52.35 | 0.00 | 26 |
| S(.)ρ(.)ψ(.) | 1492.52 | 58.30 | 0.00 | 3 |
| S(.)ρ(age*time)ψ(age) | 1493.47 | 59.26 | 0.00 | 41 |
| S(.)ρ(time)ψ(age) | 1498.99 | 64.78 | 0.00 | 22 |
| S(.)ρ(age*time)ψ(.) | 1499.85 | 65.64 | 0.00 | 40 |
| S(.)ρ(time)ψ(.) | 1505.51 | 71.30 | 0.00 | 21 |

**Supplementary Table 3.2.** Ranking of generalised linear models analysing variation in the proportion of surveys where juveniles were seen with their nest siblings across all three years of the study. Models are ranked by ΔAICc values, and weight indicates relative likelihood of each model. Null model (~1) included for comparison.

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~1 | 138.55 | 0.00 | 0.36 |
| ~ proximity to nest | 139.90 | 1.35 | 0.18 |
| ~ number of surveys | 140.58 | 2.03 | 0.13 |
| ~ year | 140.74 | 2.19 | 0.12 |
| ~ proximity to nest + number of surveys | 141.94 | 3.39 | 0.07 |
| ~ proximity to nest + year | 141.98 | 3.43 | 0.07 |
| ~ number of surveys + year | 142.78 | 4.23 | 0.04 |
| ~ proximity to nest + number of surveys + year | 144.07 | 5.52 | 0.02 |

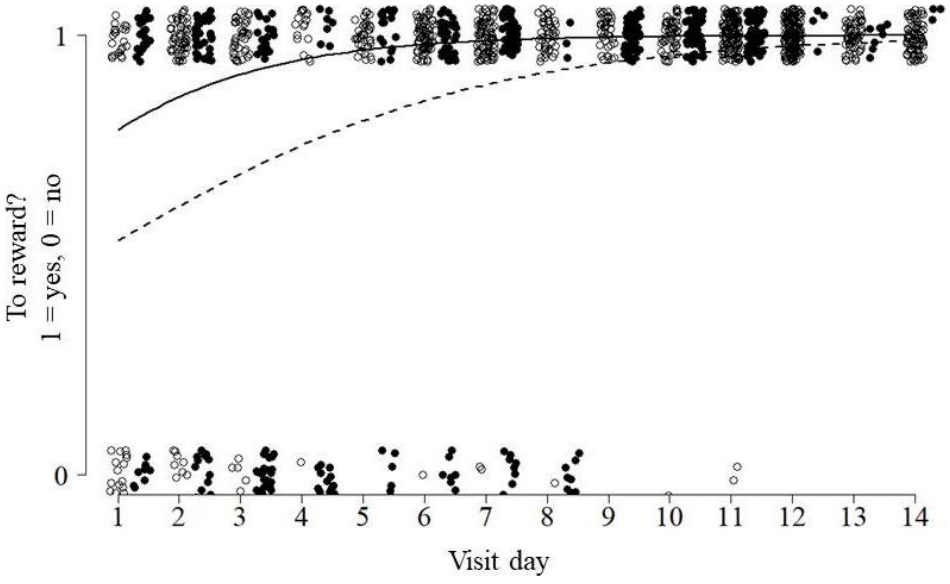



**Supplementary Figure 3.1.** Biplots of principle components analysis (PCA) showing components that explained 75% of variation: (a) PC1 and PC2, and (b) PC2 and PC3. Red arrows represent the major interactions for each component, and black dots represent individuals to show how much they engaged in each interaction, relative to others.

## *A1.3. Chapter 4 supplementary information on parent learning at nests*

Before chicks fledged, parent hihi were observed or recorded using their feeders at 21 of the 27 feeder nest sites. At the remaining six, there was no evidence of parental use. It is unlikely we missed use, due to regular observations of nest feeders. Secondly, at all nests where we did observe feeding there were multiple visits by parents within each observation session. Finally, we also checked for spots of dried sugar on feeder bases to indicate feeding activity. The reason for the lack of use was unclear but may have been due to local resource availability or variation in individual propensity to use artificial feeders, as some hihi rarely use the permanent supplementary feeding stations on Tiritiri Matangi.

First visits of side choice nest parents were random (exactly half of first visits were to the reward option across the 12 nests). They also showed no preference for the reward side across all visits on their first day (Binomial sign test: 40/66 visits to reward side, $P = 0.11$). However, as they visited over successive days, parents developed a preference for the reward side (effect of visit day = 0.42±0.04, 95% CI = 0.34 – 0.50; Supplementary Figure A1.3.1, Supplementary Table A1.3.1), with males doing so more quickly (effect of being male = 1.92±0.64, 95% CI = 0.67 – 3.18; Supplementary Figure A1.3.1, Supplementary Table A1.3.1).




**Supplementary Figure A1.3.1.** The likelihood that parent hihi (males = open circles, solid line; females = closed circles, dashed line) chose the reward side across their visits to nest feeders in the 14 days before chicks fledged. Lines of best fit calculated from the top ranked model in Supplementary Table A1.3.1.

**Supplementary Table A1.3.1.** Ranking of generalised linear models used to analyse the likelihood that parent hihi chose reward side. Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. Null model (~1) presented for comparison.

| | AICc | ΔAICc | AICc weight |
|---|---|---|---|
| ~ visit day + sex | 623.00 | 0.00 | 0.74 |
| ~ visit day | 625.12 | 2.12 | 0.26 |
| ~ sex | 750.07 | 127.08 | 0.00 |
| ~ 1 | 752.03 | 129.03 | 0.00 |

## *A1.4. Chapter 4 supplementary tables and figures*

**Supplementary Table 4.1.** Ranking of generalised linear models analysing how arrival rank varied at group site feeders for (a) all juveniles, comparing effect of feeder presence/absence; and (b) nest feeder juveniles, comparing effects of different experiences. Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. Null models (~1) are presented for comparison. Random intercept accounts for which feeder juveniles first visited (network or experiment).

(a)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ feeder presence | 860.27 | 0.00 | 1.00 |
| ~ 1 | 887.12 | 26.85 | 0.00 |

(b)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ 1 | 543.30 | 0.00 | 0.22 |
| ~ parent use | 543.50 | 0.20 | 0.20 |
| ~ feeder type | 543.75 | 0.45 | 0.18 |
| ~ used nest feeder | 544.10 | 0.80 | 0.15 |
| ~ parent use + used nest feeder | 545.40 | 2.11 | 0.08 |
| ~ feeder type + used nest feeder | 545.45 | 2.15 | 0.08 |
| ~ feeder type + parent use | 545.54 | 2.24 | 0.07 |
| ~ feeder type + parent use + used nest feeder | 547.69 | 4.39 | 0.02 |

**Supplementary Table 4.2.** Ranking of generalised linear mixed effects models analysing effect of lapse from previous bird on likelihood focal hihi chose copied their side choice, in first visits. Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. All models contain a random effect term to account for repeated records of individuals (1 | ID). Null model (~1) presented for comparison.

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ 1 | 66.71 | 0.00 | 0.57 |
| ~ lapse from previous hihi | 67.24 | 0.53 | 0.43 |

**Supplementary Table 4.3.** Ranking of (a) generalised linear models used to analyse side preference in groups; and (b) generalised linear mixed effects models analysing side preference in side choice feeder nest juveniles only. Models are ranked according to change in AICc values (ΔAICc), and the AICc weight indicates the relative likelihood of the respective model being the best model from the candidate set. For (b), all models contained a random effect term to account for repeated records of individuals (1 | ID). Null models (~1) are presented for comparison.

(a)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ experiment day*location | 466.39 | 0.00 | 1.00 |
| ~ experiment day + location | 600.09 | 133.70 | 0.00 |
| ~ location | 602.66 | 136.27 | 0.00 |
| ~ 1 | 1032.77 | 566.37 | 0.00 |
| ~ experiment day | 1034.61 | 568.22 | 0.00 |

(b)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ 1 | 318.29 | 0.00 | 0.36 |
| ~ nest feeder side | 318.46 | 0.17 | 0.33 |
| ~ experiment day | 320.30 | 2.00 | 0.13 |
| ~ nest feeder side + experiment day | 320.60 | 2.30 | 0.12 |
| ~ nest feeder side*experiment day | 322.16 | 3.86 | 0.05 |

**Supplementary Table 4.4.** Ranking of generalised linear mixed effect models analysing effects of group preference on choosing the locally-preferred side for (a) all visits, (b) when juveniles changed sites. Models contain a random effect term to account for repeated records of individuals (1 | ID) and are ranked according to ΔAICc values, so weight indicates the relative likelihood of the respective model. Only models with AICc Weight > 0.00 are presented. Null models (~1) also presented for comparison.

(a)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ group preference*age + visit day*age | 12362.94 | 0.00 | 0.31 |
| ~ group preference*age + visit day*age + time of day | 12363.43 | 0.49 | 0.24 |
| ~ group preference*age + visit day*age + focal degree | 12364.28 | 1.34 | 0.16 |
| ~ group preference*age + visit day*age + time of day + focal degree | 12364.82 | 1.88 | 0.12 |
| ~ group preference + visit day*age | 12366.60 | 3.66 | 0.05 |
| ~ group preference + visit day*age + time of day | 12367.18 | 4.24 | 0.04 |
| ~ group preference + visit day*age + focal degree | 12367.84 | 4.90 | 0.03 |
| ~ group preference + visit day*age + focal degree | 12368.46 | 5.52 | 0.02 |
| ~ group preference*age + visit day | 12370.34 | 7.40 | 0.01 |
| ~ group preference + age + visit day | 12370.37 | 7.43 | 0.01 |
| ~ group preference*age + visit day + time of day | 12370.92 | 7.98 | 0.01 |
| ~ group preference + age + visit day + time of day | 12370.97 | 8.03 | 0.01 |
| ~ group preference + age + visit day + focal degree | 12371.32 | 8.38 | 0.00 |
| ~ group preference*age + visit day + focal degree | 12371.33 | 8.39 | 0.00 |
| ~ group preference*age + visit day + time of day + focal degree | 12371.94 | 9.01 | 0.00 |
| ~ group preference + age + visit day + focal degree + time of day | 12371.95 | 9.01 | 0.00 |
| ~1 | 12645.60 | 282.66 | 0.00 |

(b)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ group preference + previous preference | 243.24 | 0.00 | 0.18 |
| ~ group preference + previous preference + time of day | 243.57 | 0.33 | 0.15 |
| ~ group preference + previous preference + visit day | 243.74 | 0.51 | 0.14 |
| ~ group preference + previous preference + visit day + site change number | 245.03 | 1.79 | 0.07 |
| ~ group preference + previous preference + site change number | 245.51 | 2.27 | 0.06 |
| ~ group preference + previous preference + time of day + focal degree | 245.90 | 2.67 | 0.05 |
| ~ group preference + previous preference + time of day + visit day + site change number | 245.91 | 2.67 | 0.05 |
| ~ group preference + previous preference + time of day + site change number | 245.93 | 2.69 | 0.05 |
| ~ previous preference + time of day + visit day + site change number | 246.07 | 2.84 | 0.04 |

| | | | |
|---|---|---|---|
| ~ group preference + previous preference + visit day + focal degree | 246.11 | 2.87 | 0.04 |
| ~ previous preference + time of day + visit day + focal degree | 246.40 | 3.17 | 0.04 |
| ~ group preference + previous preference + time of day + visit day + focal degree | 246.46 | 3.22 | 0.04 |
| ~ group preference + previous preference + visit day + site change number + focal degree | 247.44 | 4.21 | 0.02 |
| ~ previous preference | 247.57 | 4.34 | 0.02 |
| ~ group preference + previous preference + site change number + focal degree | 247.87 | 4.63 | 0.02 |
| ~ group preference + previous preference + time of day + site change number + focal degree | 248.34 | 5.10 | 0.01 |
| ~ group preference + previous preference + time of day + visit day + site change number + focal degree | 248.39 | 5.15 | 0.01 |
| ~ previous preference + time of day + visit day + site change number + focal degree | 248.49 | 5.26 | 0.01 |
| ~ previous preference + visit day + site change number + focal degree | 249.06 | 5.82 | 0.01 |
| ~ previous preference + time of day + site change number + focal degree | 250.00 | 6.76 | 0.01 |
| ~ 1 | 325.52 | 82.29 | 0.00 |

**Supplementary Table 4.5.** Ranking of generalised linear mixed effects models used to analyse site changes by juvenile hihi across the experiment. (a) length of time (lapse) between the last visit in one site and the first visit in the next site; (b) the number of site changes per day that each hihi made. Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. Null models (~1) are presented for comparison. All models included random intercept for individual identity.

(a)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ 1 | 537.88 | 0.00 | 0.67 |
| ~ lapse from previous visit in previous site | 539.32 | 1.44 | 0.33 |

(b)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~ number of site changes per day | 922.87 | 0.00 | 1.00 |
| ~ 1 | 945.27 | 22.4 | 0.00 |

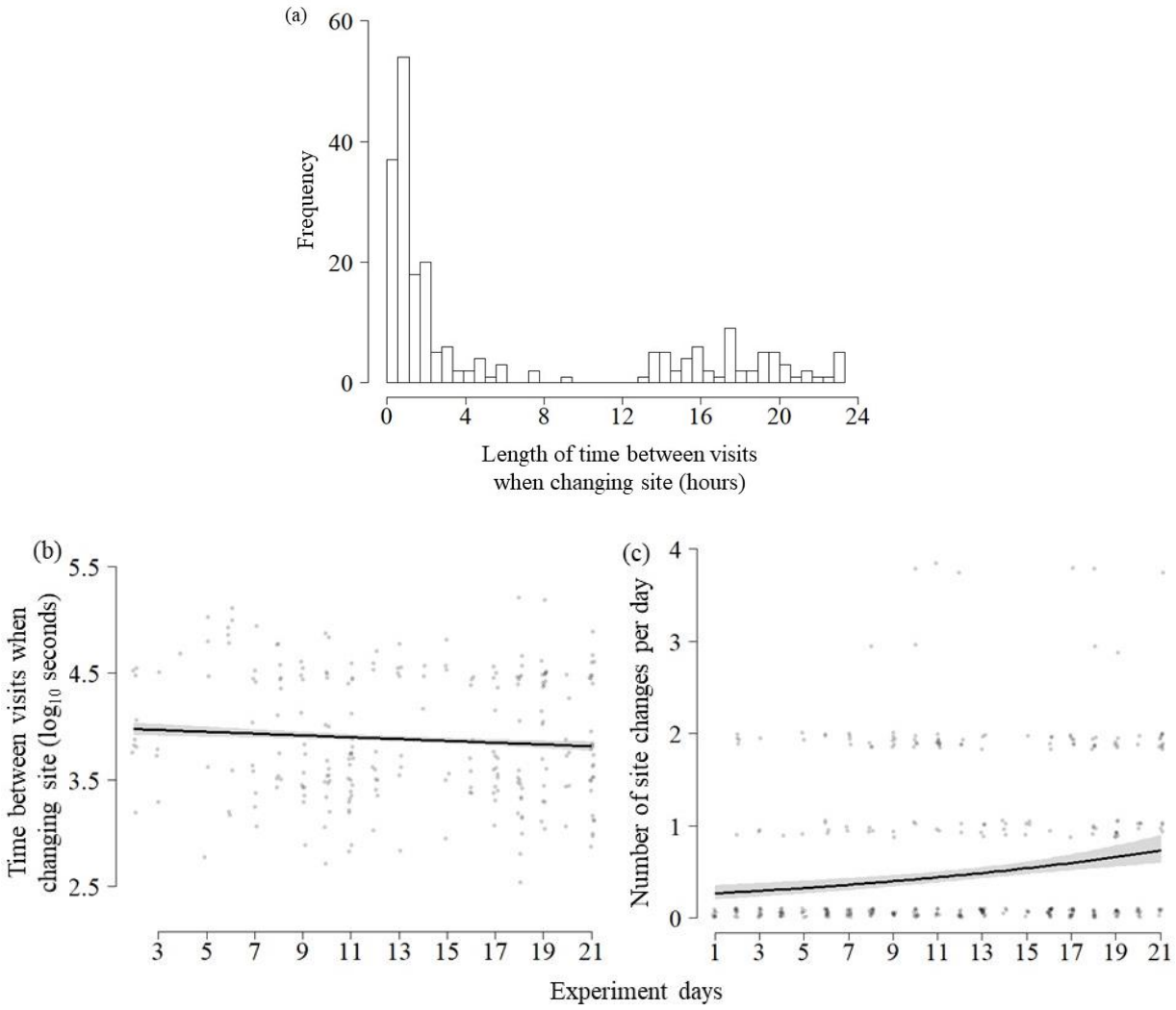
**Supplementary Table 4.6.** Ranking of generalised linear mixed effects models analysing short term effects of copying choice of preceding individual for (a) all visits, and (b) every time juveniles changed sites. All models contain a random effect term to account for repeated records of individuals (1 | ID). Models are ranked according to ΔAICc values, and the weight indicates the relative likelihood of the respective model. Only models with AICc Weight > 0.00 are presented. Null models (~1) also presented for comparison.

(a)

| | **AICc** | **ΔAICc** | **AICc Weight** |
|---|---|---|---|
| ~time since preceding hihi + group preference | 9897.32 | 0.00 | 0.34 |
| ~ time since preceding hihi + focal age + group preference | 9899.06 | 1.74 | 0.14 |
| ~ time since preceding hihi + group preference + focal degree | 9899.58 | 2.26 | 0.11 |
| ~ time since preceding hihi + group preference + tie strength | 9899.60 | 2.28 | 0.11 |
| ~ time since preceding hihi + group preference + focal age + focal degree | 9901.43 | 4.11 | 0.04 |
| ~ time since preceding + group preference + focal age*previous age | 9901.57 | 4.25 | 0.04 |
| ~ time since preceding hihi + group preference + preceding age + focal degree | 9901.57 | 4.25 | 0.04 |
| ~ time since preceding hihi + group preference + preceding age + tie strength | 9901.58 | 4.26 | 0.04 |
| ~ time since preceding hihi + group preference + focal degree + tie strength | 9901.94 | 4.62 | 0.03 |
| ~ time since preceding hihi + group preference + preceding age + focal age + tie strength | 9903.45 | 6.13 | 0.02 |
| ~ time since preceding hihi + group preference + focal age + preceding age + focal degree | 9903.46 | 6.14 | 0.02 |
| ~ time since preceding hihi + group preference + focal age + focal degree + tie strength | 9903.86 | 6.54 | 0.01 |
| ~ time since preceding hihi + group preference + preceding age + focal degree + tie strength | 9904.01 | 6.69 | 0.01 |
| ~ time since preceding hihi + group preference + tie strength + focal age*preceding age | 9904.06 | 6.74 | 0.01 |
| ~ time since preceding hihi + group preference + focal degree + focal age*preceding age | 9904.08 | 6.76 | 0.01 |
| ~ 1 | 9977.16 | 79.84 | 0.00 |

(b)

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~1 | 335.30 | 0.00 | 0.14 |
| ~ group preference | 335.40 | 0.10 | 0.13 |
| ~ time since preceding hihi | 336.50 | 1.19 | 0.08 |
| ~ time since preceding hihi + group preference | 336.77 | 1.47 | 0.07 |
| ~ tie strength | 336.90 | 1.60 | 0.06 |
| ~ site change number | 337.20 | 1.90 | 0.05 |
| ~ group preference + tie strength | 337.41 | 2.10 | 0.05 |
| ~ preceding age | 337.68 | 2.38 | 0.04 |
| ~ focal degree | 337.72 | 2.41 | 0.04 |
| ~ group preference + preceding age | 337.98 | 2.68 | 0.04 |
| ~ group preference + focal degree | 338.01 | 2.70 | 0.04 |
| ~ time since preceding hihi + tie strength | 338.43 | 3.13 | 0.03 |
| ~ time since preceding hihi + preceding age | 339.02 | 3.71 | 0.02 |
| ~ time since preceding hihi + focal degree | 339.09 | 3.79 | 0.02 |
| ~ group preference + time since preceding hihi + tie strength | 339.11 | 3.80 | 0.02 |
| ~ preceding age + tie strength | 339.44 | 4.13 | 0.02 |
| ~ group preference + time since preceding hihi + preceding age | 339.52 | 4.21 | 0.02 |
| ~ focal degree + tie strength | 339.53 | 4.22 | 0.02 |
| ~ group preference + time since preceding hihi + focal degree | 339.58 | 4.28 | 0.02 |
| ~ group preference + preceding age + tie strength | 340.17 | 4.86 | 0.01 |
| ~ group preference + focal degree + tie strength | 340.23 | 4.93 | 0.01 |
| ~ preceding age + focal degree | 340.27 | 4.97 | 0.01 |
| ~ group preference + preceding age + focal degree | 340.79 | 5.48 | 0.01 |
| ~ time since preceding hihi + preceding age + tie strength | 341.13 | 5.82 | 0.01 |
| ~ time since preceding hihi + focal degree + tie strength | 341.26 | 5.95 | 0.01 |
| ~ time since preceding hihi + preceding age + focal degree | 341.81 | 6.51 | 0.01 |




**Supplementary Figure 4.1.** (a) frequency of number of hours between visits when juveniles changed sites, for all site changes that occurred in less than 24 hours (90% of changes); (b) Time (log10-transformed seconds) between visits when changing sites over days of the experiment; (c) the number of site changes individual hihi made over days of the experiment. Predicted model estimates and 95% confidence intervals (grey areas) come from the top-ranked models analysing site changes over days.

## *A1.5. Chapter 5 supplementary tables*

**Supplementary Table 5.1.** Ranking by QAICc of all models to explain variation in inter-survey survival (ϕ) depending on sex and time, with and without covariate (degree rank change) for (a) translocated and (b) non-translocated hihi. Models also account for variation in re-sighting likelihood (ρ).

(a)

| Model | QAICc | ΔQAICc | Model likelihood | Number of parameters |
|---|---|---|---|---|
| ϕ(sex+rankchange)ρ(sex) | 159.91 | 0.00 | 1.00 | 5 |
| ϕ(.)ρ(sex) | 160.25 | 0.34 | 0.85 | 3 |
| ϕ(sex)ρ(sex) | 160.93 | 1.02 | 0.60 | 4 |
| ϕ(.)ρ(.) | 161.13 | 1.22 | 0.54 | 2 |
| ϕ(time+rankchange)ρ(sex) | 163.04 | 3.13 | 0.21 | 8 |
| ϕ(time)ρ(sex) | 163.32 | 3.41 | 0.18 | 7 |
| ϕ(sex+time+rankchange)ρ(sex) | 163.64 | 3.72 | 0.16 | 9 |
| ϕ(sex+time)ρ(sex) | 164.14 | 4.23 | 0.12 | 8 |
| ϕ(time+rankchange)ρ(time) | 166.49 | 6.58 | 0.04 | 10 |
| ϕ(time+rankchange)ρ(sex+time) | 166.88 | 6.96 | 0.03 | 12 |
| ϕ(sex+time+rankchange)ρ(sex+time) | 168.85 | 8.94 | 0.01 | 13 |
| ϕ(time+rankchange)ρ(sex+time+rankchange) | 169.12 | 9.21 | 0.01 | 13 |
| ϕ(sex+rankchange)ρ(sex+time) | 169.47 | 9.56 | 0.01 | 10 |
| ϕ(sex+rankchange)ρ(time) | 169.78 | 9.87 | 0.01 | 9 |
| ϕ(.)ρ(sex+time) | 169.87 | 9.96 | 0.01 | 8 |
| ϕ(time)ρ(sex+time) | 170.05 | 10.14 | 0.01 | 11 |
| ϕ(.)ρ(time) | 170.44 | 10.53 | 0.01 | 7 |
| ϕ(sex+time+rankchange)ρ(time) | 170.54 | 10.63 | 0.00 | 12 |
| ϕ(sex)ρ(time) | 170.68 | 10.77 | 0.00 | 8 |
| ϕ(sex)ρ(sex+time) | 170.78 | 10.87 | 0.00 | 9 |
| ϕ(sex+time+rankchange)ρ(sex+time+rankchange) | 171.14 | 11.23 | 0.00 | 14 |
| ϕ(.)ρ(sex+time+rankchange) | 171.50 | 11.59 | 0.00 | 9 |
| ϕ(sex+rankchange)ρ(sex+time+rankchange) | 171.58 | 11.67 | 0.00 | 11 |
| ϕ(time)ρ(time) | 171.58 | 11.67 | 0.00 | 10 |
| ϕ(sex+time)ρ(time) | 171.91 | 12.00 | 0.00 | 11 |
| ϕ(sex+time)ρ(sex+time) | 171.97 | 12.06 | 0.00 | 12 |
| ϕ(time)ρ(sex+time+rankchange) | 172.19 | 12.28 | 0.00 | 12 |
| ϕ(sex)ρ(sex+time+rankchange) | 172.47 | 12.56 | 0.00 | 10 |
| ϕ(sex+time)ρ(sex+time+rankchange) | 176.53 | 16.62 | 0.00 | 14 |
| ϕ(sex*rankchange+time*rankchange) ρ(sex*rankchange+time*rankchange) | 198.11 | 38.20 | 0.00 | 26 |

(b)

| Model | QAICc | ΔQAICc | Model likelihood | Number of parameters |
|---|---|---|---|---|
| ϕ(time)ρ(sex+time) | 124.53 | 0.00 | 1.00 | 7 |
| ϕ(.)ρ(sex+rankchange+time) | 124.69 | 0.16 | 0.92 | 7 |
| ϕ(.)ρ(sex+time) | 124.75 | 0.22 | 0.90 | 6 |
| ϕ(time)ρ(sex+rankchange+time) | 125.12 | 0.59 | 0.74 | 8 |
| ϕ(time)ρ(time) | 125.60 | 1.07 | 0.59 | 6 |
| ϕ(sex+time)ρ(time) | 125.93 | 1.41 | 0.50 | 7 |
| ϕ(.)ρ(time) | 126.18 | 1.66 | 0.44 | 5 |
| ϕ(sex+rankchange)ρ(sex+time) | 126.32 | 1.80 | 0.41 | 8 |
| ϕ(.)ρ(sex) | 126.39 | 1.86 | 0.39 | 3 |
| ϕ(rankchange+time)ρ(sex+time) | 126.42 | 1.89 | 0.39 | 9 |
| ϕ(rankchange+time)ρ(sex) | 126.62 | 2.09 | 0.35 | 6 |
| ϕ(sex+time)ρ(sex+time) | 126.79 | 2.26 | 0.32 | 8 |
| ϕ(sex)ρ(sex+rankchange+time) | 126.93 | 2.41 | 0.30 | 8 |
| ϕ(sex)ρ(sex+time) | 126.96 | 2.43 | 0.30 | 7 |
| ϕ(.)ρ(.) | 126.99 | 2.46 | 0.29 | 2 |
| ϕ(sex+rankchange)ρ(time) | 127.07 | 2.54 | 0.28 | 7 |
| ϕ(rankchange+time)ρ(time) | 127.22 | 2.69 | 0.26 | 8 |
| ϕ(time)ρ(sex) | 127.25 | 2.72 | 0.26 | 5 |
| ϕ(sex)ρ(time) | 127.34 | 2.81 | 0.25 | 6 |
| ϕ(sex+time)ρ(sex+rankchange+time) | 127.45 | 2.92 | 0.23 | 9 |
| ϕ(sex+rankchange)ρ(sex+rankchange+time) | 127.72 | 3.19 | 0.20 | 9 |
| ϕ(sex+rankchange)ρ(sex) | 127.72 | 3.19 | 0.20 | 5 |
| ϕ(rankchange+time)ρ(sex+rankchange+time) | 127.99 | 3.46 | 0.18 | 10 |
| ϕ(sex)ρ(sex) | 128.26 | 3.73 | 0.15 | 4 |
| ϕ(sex+rankchange+time)ρ(sex) | 128.32 | 3.79 | 0.15 | 7 |
| ϕ(sex+rankchange+time)ρ(time) | 128.35 | 3.82 | 0.15 | 9 |
| ϕ(sex+time)ρ(sex) | 128.62 | 4.09 | 0.13 | 6 |
| ϕ(sex+rankchange+time)ρ(sex+time) | 128.76 | 4.23 | 0.12 | 10 |
| ϕ(sex+rankchange+time)ρ(sex+rankchange+time) | 130.35 | 5.83 | 0.05 | 11 |
| ϕ(sex*rankchange+time*rankchange) ρ(sex*rankchange+time*rankchange) | 134.59 | 10.06 | 0.01 | 16 |

# APPENDIX 2: VALIDATION OF METHODS

Various analyses to understand strengths and weaknesses of my recording methods used in Chapters 3 and 4 are summarised below, with mention of the Chapters to which each analysis applies.

## *A2.1. Comparison of PIT tag and observation data*

### BACKGROUND

Previous studies have suggested that networks generated using different techniques may not produce comparable sociability measures (Castles et al., 2014). Between Chapters, I used two different methods of collecting network data: observations (Chapters 3; 5), and PIT tags (Chapter 4; used in one year only to remotely record visits to feeders). Thus, I compared sociability of individuals in the two networks to better understand the comparability of these networks across Chapters.

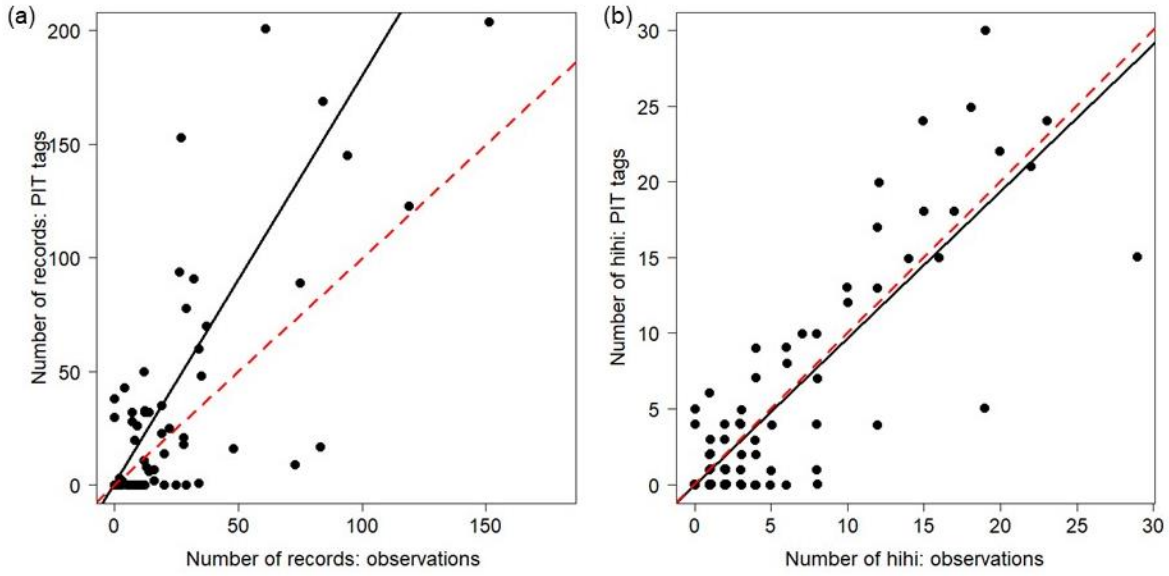
### METHODS

In one field season (2016), I used both PIT tag and observations to record the presence and behaviour of juveniles in groups. Thus, I compared number of individuals captured in data, and the social characteristics the data defined, between observational and PIT tag data over the period when feeders were present in group sites (7$^{th}$ Feb – 6$^{th}$ April 2016). This provided a cross-reference to assess if the two networks represented similar patterns in the individuals present in groups and their interactions (and thus, were both datasets more likely to be reliable). It also provided evidence of the number of birds present over a longer time period than just the hour-long surveys, to assess if my survey method was likely to be representing birds present in group sites each day (Chapter 3).

### ANALYSIS AND RESULTS

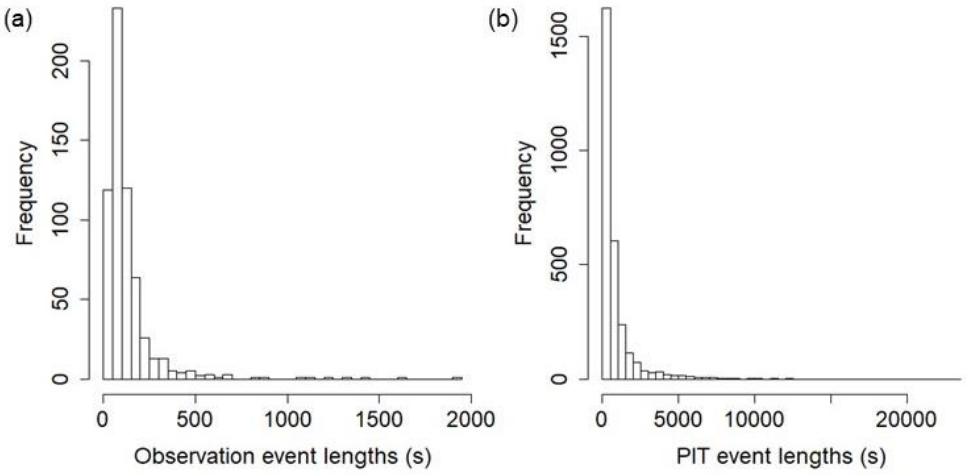
First, I compared (1) number of hihi and (2) number of records recorded in each 1-hour survey in each site while feeders were present (see Chapter 4), and recorded across the duration of the same day of each survey by PIT tags at feeders. There was strong correlation in numbers between each of the two methods (Supplementary Figure A2.1.1; Spearman's rank correlation: number of records, $S$ = 20789, $rho$ = 0.72, $P$ < 0.001; number of hihi, $S$ = 22530, $rho$ = 0.69, $P$ < 0.001). Overall, there was no significant difference in number of birds recorded by the two methods each day (paired Wilcoxon signed rank test: $V$ = 1278.5, $P$ = 0.834), but there were more records captured by PIT tags than observations (paired

Wilcoxon signed rank test: $V = 846.5$, $P = 0.006$). This difference was not surprising, considering the PIT tag readers were recording throughout the day (approx. 13 hours per day), while surveys only took place for one hour. While this highlighted how the methods differed, overall the relative trends were consistent: busier days recorded more hihi and more records for both methods. No difference in the numbers of birds recorded suggested that collecting data on a coarser scale with 1-hour observations still accurately represented the number of birds present at a site that day.

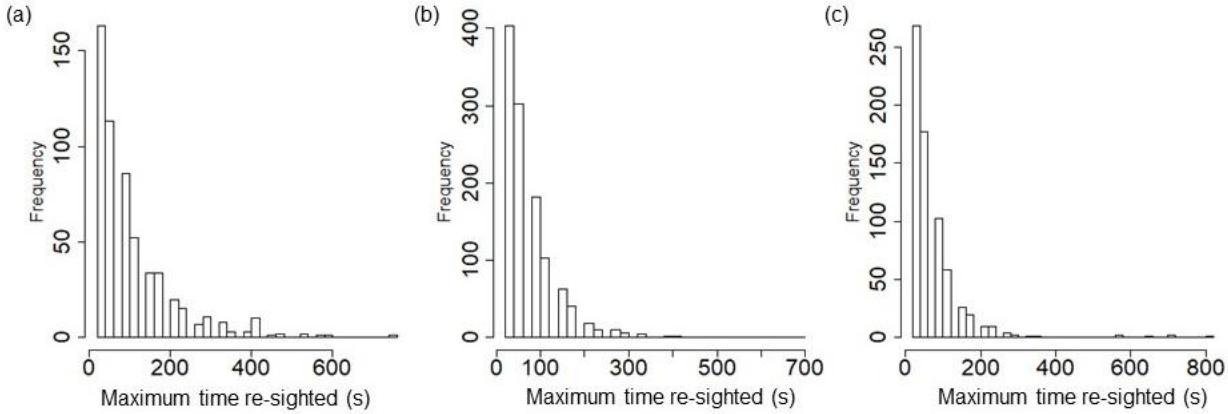



**Supplementary Figure A.2.1.1.** Correlation between the number of (a) records and (b) individual hihi recorded by 1-hour observations in group sites and PIT-tag recorders at feeders across the entire length of the same day of survey. Red dashed line represents 1:1 correlation, and black line represents correlation calculated from Spearman's rank analysis.

I also compared sociality metrics from networks generated using the two methods, used in Chapter 3 (observation network) and Chapter 4 (PIT tag network). Both networks were constructed using the "gmmevents*"* function in the R package asnipe (Farine, 2013). First, I compared the event windows generated by "gmmevents" to create associations, as the length of these windows is used to define associations so different length windows would allow for different association opportunities. There were approximately five times the number of event windows calculated from the PIT tag data compared to observation data (Supplementary Figure A2.1.2). Additionally, PIT tag data event windows were longer length, although in both methods the majority of event windows were < 900s (Supplementary Figure A2.1.2; median time length of event windows in observation data = 90s; median length PIT tag data = 434s; Wilcoxon rank sum test: $W = 245890$, $P < 0.001$). Both methods recorded event lengths that were longer than the maximum time I had re-sighted individual hihi in the original observation data (15 minutes, Supplementary Figure A2.1.3).



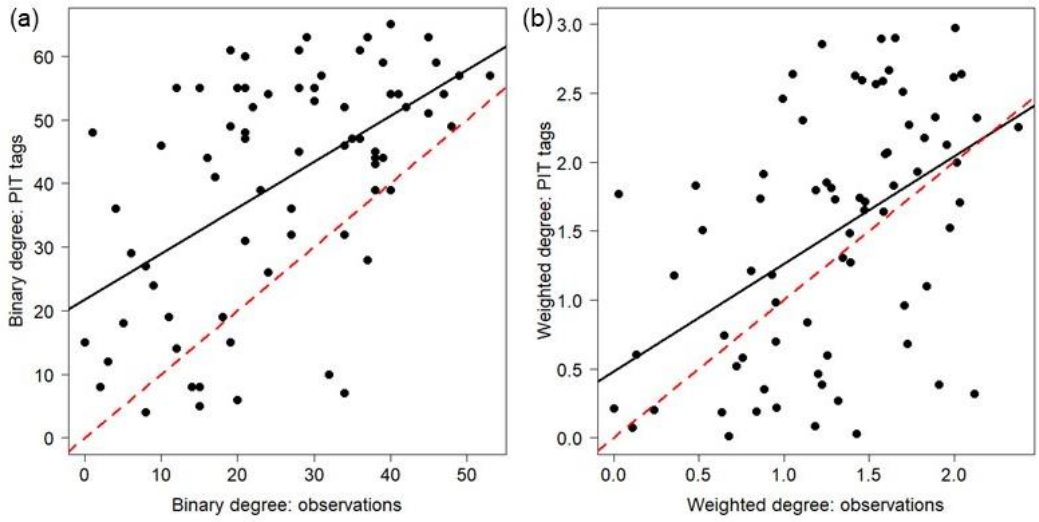

**Supplementary Figure A2.1.2.** Histogram of frequency of different event lengths generated using asnipe package to construct networks from (a) observation data and (b) PIT tag data collected in 2016.




**Supplementary Figure A2.1.3.** Histogram of frequency of different maximum re-sighting times for individual hihi from the observation data recorded in group sites for Chapter 4, recorded (a) before feeder setup (detecting group sites); (b) while the network feeder was in place; and (c) while the side choice feeder was in place. Times defined as observation blocks where I repeatedly saw individuals, so are recorded to the nearest 30s.

As event window lengths defined associations and longer windows had the potential to affect individual sociality scores, I compared degree values per individual generated from the two different networks. More sociable birds in the PIT tag network were also more sociable in the observation network (Supplementary Figure A2.1.4; binary degree: $S = 31763$, $rho = 0.51$, $P < 0.001$; weighted degree: $S = 32796$, $rho = 0.49$, $P < 0.001$). However, a hihi's degree score (weighted and binary) was generally 50%

larger in PIT tag networks compared to observation networks. This was likely due to the smaller timespan for surveys compared to PIT tag recordings. The more constrained timings allocated to hihi using 30 second observation blocks (Chapter 3) also could have meant their association windows were more clearly defined by "gmmevents". Even with some variation, the overall correlation suggests that both types of networks could be implicated in similar ways when considering the importance of sociability for social information transmission: irrespective of the data collection method, more sociable birds remained more sociable and so could interact with more sources of social information.




**Supplementary Figure A2.1.4.** Correlation between (a) binary degree (number of associates) and (b) weighted degree (number of associates and strength of associations) generated from observation and PIT tag network. Red dashed line represents 1:1 correlation, and black line represents correlation calculated from Spearman's rank analysis.

## *A2.2. Using camera traps to validate PIT tag data*

**BACKGROUND**

There is a growing movement in using remote recording equipment to collect detailed and extensive data to research questions on animal behaviour (Farine & Whitehead 2015). However, to date, there are few examples where researchers have validated data collected using bio-logging technology (Boyland et al., 2013; Levin et al., 2015), especially PIT tags. This presents two problems. The first is the assumption that recordings represent meaningful behaviours and associations between animals. Secondly, the efficacy of the recording equipment is rarely evaluated but needs to be to understand the extent of conclusions that can be made (for example, in social network analysis).

**METHODS**

During the experiment in Chapter 4, I recorded feeder visits at my two experimental feeders set up in groups using both PIT-tag recorders at feeder entrances, and camera traps positioned approximately ½m from the feeder entrances. Visits were recorded by PIT-tags by using antennae at feeder entrance holes, and camera traps were records 30 second video clips once triggered by infrared detection of bird presence. The camera trap model (Bushnell NatureView HD Max ®) is designed to be sensitive enough to detect small garden wildlife and thus was capable of recording hihi visits. Both recording methods produced time-stamped records. For both feeders, I selected a subsample of videos to analyse by dividing all recording days into half-day segments, then selecting 10 segments at random (using a random number generator where each segment was numbered concurrently). Within each segment, I then randomly selected three videos. In each video, I identified the first hihi to enter the feeder (when it passed through an antenna loop into the feeder) by its colour-ring combination and recorded the time and date of its entry. If no hihi were recorded in that video, I moved on to the next video in that same slot. Any videos where hihi were unidentifiable were also discounted. Next, I checked if there was a corresponding recording of entry by the same individual in the PIT tag data. Entries were assumed to be the same if there were records to within 5 seconds. If there were matching records, that entry was assigned a "1"; if they did not match, "0".

**ANALYSIS AND RESULTS**

I recorded entries in 48 videos from Site 1 and Site 2 each (Site 1: 18 individuals; Site 2: 27 individuals). I analysed likelihood of detection across days since set-up (1-21), experimental stage (network feeder or side-choice feeder, see Chapter 4), and between locations (Site 1 and Site 2) and included an interaction term between day and stage because stages were run sequentially. I used binominal Generalised Linear Mixed Effect Models (GLMMs) with a random intercept term for individual to account for repeated visits by the same birds. I used model-averaging with the R package AICcmodavg to rank models by their corrected Akaike Information Criterion (AICc) values, and for any models with $\Delta$AICc < 2 I used model averaging to calculate effect sizes of included parameters. However, the null model was the highest ranked (Supplementary Table A.2.2.1) which suggested the likelihood of a visit being detected on PIT tags did not vary across days, experiment stages, or between the two sites. Overall mean recorded proportion of camera trap visits by PIT tags was 0.65±0.07 at Site 1, and 0.60±0.07 at Site 2. Next, I used entries recorded at the side choice feeders (Site 1: 29 entries; Site 2 = 25 entries) to analyse if there were differences in entry detecting between the two side choices. Using a Fisher's exact test, there was no difference in the proportions of visits recorded in either Site (Fisher's exact test; Site 1: $N = 29$, $P = 0.451$; Site 2: $N = 25$, $P = 0.111$).

Together, these results mean that at any given visit, an individual was detected 60 – 65% of the time, but detection was equally likely on either side of each feeder and did not change across the experiment. Therefore, the side choice patterns observed in Chapter 4 were unlikely to have been affected by detection. Patterns in group level preference may have also been stronger in reality.

**Supplementary Table A2.2.1.** Ranking of binomial GLMM models analysing variation in detection of PIT tag entries in comparison to entries recorded by camera traps. All models contain a random intercept term for individuals. Models are ranked according to ΔAICc values.

| | AICc | ΔAICc | AICc Weight |
|---|---|---|---|
| ~ 1 | 123.53 | 0.00 | 0.26 |
| ~ day | 123.66 | 0.13 | 0.24 |
| ~ day + experiment stage | 124.62 | 1.09 | 0.15 |
| ~ stage | 125.37 | 1.84 | 0.10 |
| ~ location | 125.80 | 2.27 | 0.08 |
| ~ day + location | 125.99 | 2.46 | 0.08 |
| ~ day + stage + location | 127.04 | 3.51 | 0.04 |
| ~ stage + location | 127.76 | 4.23 | 0.03 |
| ~ day*stage + location | 129.37 | 5.84 | 0.01 |

**APPENDIX 2 REFERENCES**

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# APPENDIX 3: GRANT REPORT

This Appendix contains a report published by the British Ornithologist's Union for a grant I received in 2015. It describes a minor extra study I conducted during my PhD to investigate the importance of social connections for food-finding and overwinter survival of juvenile hihi.